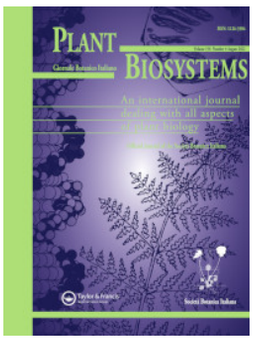

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Impact of drying temperature on tissue anatomy and cellular ultrastructure of different aromatic plant leaves

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ABSTRACT

Herbs are processed by drying to decrease the moisture content and therefore to inhibit the growth of microorganisms, reducing the alterations during the storage and creating shelf-stable products. The drying of aromatic herbs has been carried out over the years as convective drying with hot air but information on the impact of this process at cellular level is still limited. In this work, conventional hot-air drying technique was compared to a cold drying method emerging in recent years to evaluate the cellular damages in four economically important aromatic herbs such as lemon balm, mint, mallow and savory. Results suggest that the two applied drying technologies differently affect the cellular structure in the diverse species, representing a basis for future researches in the optimization of the whole process and in decision making.

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Introduction

A growing consumers' interest in organic and herbal-based products has led to an increased demand in the industry of medicinal and aromatic plants (MAPs) in the past ten years (Aftab and Hakeem 2020). MAPs are primarily used for therapeutic, aromatic and/or culinary purposes as components of cosmetics, medicines, health foods and other natural health products. They are also the starting materials for value-added processed natural ingredients such as essential oils (Giannenas et al. 2020). Depending on the final use, MAPs may be traded as raw or processed materials. To address the modern consumer's demands for natural, safe, and high-quality products and to meet legislative regulations, industry must improve and monitor all the production steps. To produce high-quality herbal products, attention must be paid to many factors, among them the transformation processes and in particular the storage (Tanko et al. 2005). Drying is the most common way to preserve MAPs. The decrease of plant moisture content is the first step in many postharvest operations and is aimed at preventing enzymatic and microbial activity and therefore preserving the product and extending shelf life (Pandey and Savita 2017; Thamkaew et al. 2020). Several drying methods have been developed in the past 20 years with the aim of improving both quality and efficiency of the drying process. Notably, the energy demand of drying represents a significant cost factor in MAPs production, being 30%–50% of the total costs. Therefore, fine-tuning of operational methods and energy use is crucial for an optimal drying process (Müller 2007; Motevali et al. 2011; Taner 2015; Jin et al. 2018). The most popular and common method is oven-drying (also called convective drying or hot-air drying) in which the drying temperature usually ranges between 40 °C and 60 °C (Thamkaew et al. 2020). However, high drying temperature may have undesirable effects on the quality of dried product. Low drying temperatures are generally recommended to preserve the aromatic/functional compounds of MAPS, but, as a result, the drying time is longer and energy efficiency is lower. To increased dryer capacity, drying temperature should be as high as possible without reducing the quality of the product (Müller 2007). Maximum allowable temperatures depend on the different plant species and on the characteristic to be preserved, which may depend on the dried herb usage (Jin et al. 2018). For instance, the preservation of bioactive compounds is central for plants used for medical purposes, while the colour and fresh-like characteristic aroma are key factors for culinary dried herbs (Thamkaew et al. 2020). The impact of drying air temperature has been investigated mainly on active ingredients, sometimes considering the total amount of essential oil, sometimes specific components, showing increasing essential-oil losses with increasing temperature, but with different temperature sensitivity between species (Müller

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2007). Few studies have taken into consideration the anatomical changes caused by different temperatures during the drying process (van't Hag et al. 2020). In this work, performed in the frame of the project «L'innovazione di processo nella filiera delle erbe aromatiche essiccate - ESSICA» (Interreg V France-Italy, ALCOTRA 2014-2020), we present the analysis of the impact of two drying methods (conventional at 40 °C and with dehydrated cold air at 20 °C) on the leaf structure at cellular and subcellular level of four aromatic plants.

Materials and methods

Plant species and growth conditions

Work was done on four aromatic plant species: mallow (*Malva sylvestris* L., Malvaceae), lemon balm (*Melissa officinalis* L., Lamiaceae), mint (*Mentha piperita* L./*Mentha spicata* L., Lamiaceae), savory (*Satureja hortensis* L., Lamiaceae). Plants were grown in open field by farmers of Cooperativa Pancalieri (Torino, Italy) in 2019, under the management used for commercial purpose. Harvest was done during summer for lemon balm, mint and savory, and in September for mallow.

Drying

Two different drying procedures were tested: (1) traditional drying, i.e., 40 °C for 24 h using a Memmert UF110 oven (Schwabach, Germany) and (2) cold drying, i.e., 20 °C, 48 h or 72 h for mallow (according to the time necessary for the herb to reach a humidity lower than 12%), using a Northwest Technologies NWT100 dryer (Boves, Italy) where a continuous flow of cold dehydrated air is obtained thanks to the action of cooling coils that freeze the water extracted from the herbs. The reached humidity was always less than 12%. Plants have been dried soon after harvesting, to avoid storage effects. During the drying process a sampled branches has been kept on a flat surface, avoiding as much as possible leaf crumpling for a more accurate sampling. Samples have been then carefully placed in plastic bags to avoid leaves breakages. Dried samples have been also compared with fresh samples directly collected from a plant grown in the same field.

Color determination

The four aromatic herbs were submitted to color determination to evaluate any differences due to the different drying method used. Three biological replicates were analysed for each herb and for both drying techniques. The color analysis was conducted in transmittance mode on a CM-5 spectrophotometer (Konica Minolta, Tokyo, Japan). L*, a*, and b* CIELab parameters were used to measure the color, where L* is a coefficient of lightness ranging from 0 (black) to 100 (white), a* indicates the colors red-purple (when positive a*) and bluish-green (when negative a*), and b* denotes the colors yellow (when positive b*) and blue (negative b*). The ΔE parameter, which represents the difference between two colors (Hill et al. 1997) and its perceptibility by the human eye when $\Delta E > 2.5$, was calculated according to the equation

Microscopical analysis

Leaf pieces were collected from both fresh and dried plants, trying to choose, whenever possible, comparable leaf areas. Samples were fixed in 2.5% glutaraldehyde in 10 mM phosphate buffer pH 7.2, dehydrated with an increasing series of ethanol (30%, 50%, 70%, 90% and 100%), followed by 100% acetone and embedded in Epon/Araldite resin, following a standard protocol. The resin was polymerized for 24 h at 60 °C. Embedded samples were processed for ultramicrotomy. For each thesis, twelve leaf pieces were embedded. For optical microscopical observations, 1 µm thick sections were cut and stained with 1% Toluidine Blue and slides were observed by a Leica microscope equipped with a camera. Picture were taken by mean of the Leica Lab software.

For transmission electron microscopy, 50 nm ultrathin sections were obtained and subjected to double contrast with lead citrate and uranyl acetate. Observations were performed on a CM10 transmission electron microscope (Philips Electronics, Eindhoven, The Netherlands).

Results and discussion

In this work, the two main drying techniques (traditional and cold) were compared to evaluate the cellular damages in four economically important aromatic herbs such as lemon balm, mint, mallow and savory. The impact on morphological features might also mirror differences in derivate compounds related to their medical, flavoring and aromatic qualities. It is worth noting that the drying temperature plays an important role on the preservation of volatile compounds of dried herbs after the drying process (Thamkaew et al. 2020). Several studies on herb-drying methods were performed with the aim to improve the quality of commercial dried herbs that generally is lower than fresh herbs (Thamkaew et al. 2020). Stereomicroscopic observations of the leaf lamina of the four considered plant species showed a different grade of green color, suggesting also a different impact of the two drying protocols mainly for mint and balm lemon (unshown). As aromatic and medicinal plant species are used as tea, color is an essential quality criterion since it appears to consumers (Müller and Heindl 2006). The color degradation in dried herbs is due to the degradation of pigments (i.e., chlorophyll and anthocyanin), and the degradation of chlorophylls in green herbs is the most common change that was reported to occur during the drying process (Thamkaew et al. 2020). Here, a different color of dried leaves was evident (Figure 1), depending on the applied drying method and the considered species. The colorimetric analysis was based on ΔE parameter calculation which determines whether two colors can be distinguished by the human eye ($\Delta E > 2.5$). The results showed that for all herbs the color of the product obtained with cold drying was different from that obtained with the

A

B

Aromatic herb	ΔE
Melissa officinalis L.	4.18
Mentha spp.	2.68
Malva sylvestris L.	2.83
Satureja hortensis L.	3.98

Figure 1. Difference between colors in the herbs dried following the two drying methods. A, *Melissa officinalis* L. chopped leaves treated with cold (left) and traditional (right) drying; B, ΔE parameter, that represents the difference between two colors (Hill et al. 1997), calculated for each herb treated with traditional and cold drying.

traditional method. In particular, the cold dried samples tended to show higher brightness values and a greater tendency to green and yellow (data not shown). Despite biochemical data are not available, a different impact on pigment contents may be suggested, as confirmed by the alteration in chloroplast structure observed by the electron microscopy (see below). It has been already reported that the release of chlorophyll molecules from the protein complex, which could promote the transformation of chlorophylls into pheophytins due to heat exposure, could also lead to the releasing of substrates for enzymatic browning reactions to the surrounding areas (Thamkaew et al. 2020). This could justify the higher brightness observed in the cold dried leaves with respect to that obtained with the traditional method.

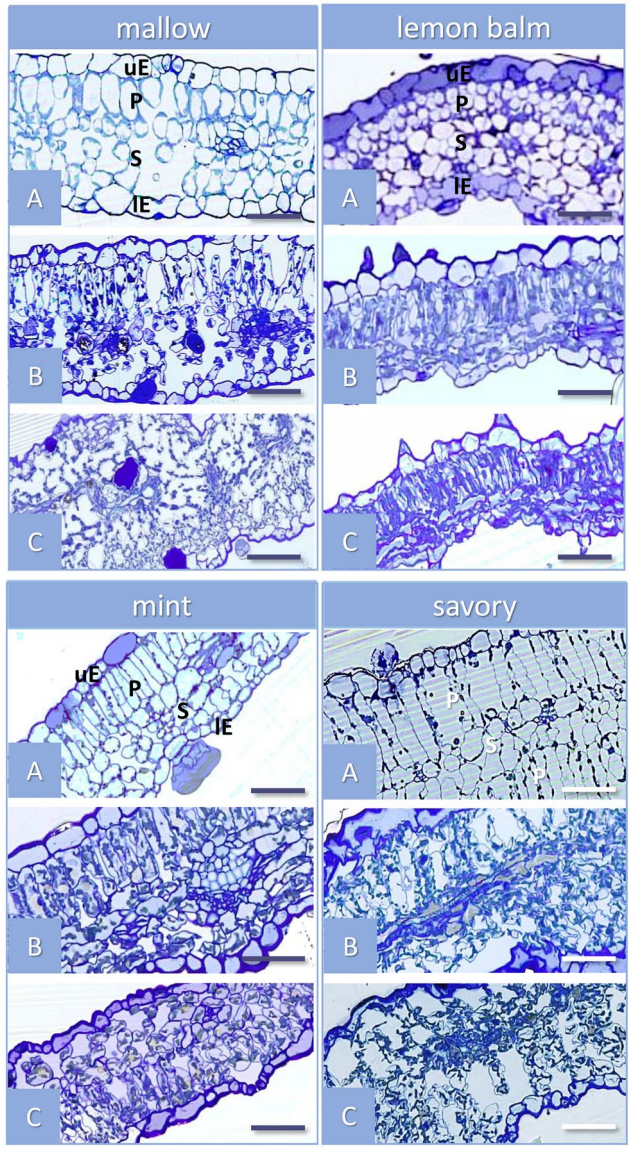

Figure 2. Semithin cross sections (stained with Toluidine blue) of leaves from the different plant species used in this study: panels A, fresh leaves; panels B, conventionally dried leaves; panels C, cold dried leaves. In *Malva sylvestris* L. (mallow), *Melissa officinalis* L. (lemon balm) and *Mentha* spp. (mint) tissue organization is the same, with an upper epidermis (uE), a palisade mesophyll (P), a spongy mesophyll (S) and a lower epidermis (lE). In *Satureja hortensis* L. (savory), under each epidermis there is a layer of palisade cells (P) separated in the middle by a layer of spongy tissue (S). For further description see text. All bars = 70 µm.

Optical microscopy observations

To verify the impact of the two technologies at cellular level, optical and transmission electron microscopy observations were performed. Microscopic observation of semithin sections showed a change in leaf anatomy due to the drying process in all the plant considered, however to different extent. Anatomical variations mainly concerned a loss in the regular arrangement of the leaf tissues, loss of the cell shape and chloroplast displacement (Figure 2). Fresh leaves showed the typical tissue layers (Figure 1, panel A), that is to say: upper epidermis, palisade mesophyll, spongy mesophyll, lower epidermis for mallow (Romitelli and Martins 2013), lemon balm (Yen et al. 2017), mint (Oliveira et al. 2017) and upper epidermis, palisade mesophyll, spongy mesophyll, palisade mesophyll, lower epidermis for savory (Satil et al. 2002). In mallow leaves, after drying, tissues appeared disorganized with irregular cell shape and chloroplasts misplaced (Figure 2, panels B, C). The traditional drying method apparently had a milder effect, since all leaf tissues were easily recognizable and the cell shape quite regular (Figure 2, panel B). Instead, in cold dried samples, tissues were severely disorganized and almost unrecognizable, except for the epidermis (Figure 2, panel C). In the case of lemon balm, tissue organization was not dramatically affected by drying at both temperatures. Only parenchyma mesophyll cells appeared particularly

shrunken and, as a consequence, with a dense protoplasm (Figure 2, panels B, C).

As regards mint leaves, again no striking differences were observed after both drying methods. Although chloroplasts were misplaced, cell shape and tissue arrangement were only slightly affected (Figure 2, panels B, C). Finally, savory leaves, probably due to their small size and narrow shape, were the most sensitive to dryings: both temperatures dramatically changed cellular shape, chloroplast localization and tissue organization (Figure 2, panels B, C).

Electron microscopy observations

Although several papers describe the ultrastructural modifications during leaf senescence, few data were obtained on the impact of drying at cellular level (van't Hag et al. 2020). Ultrastructure analysis of herb leaves confirmed and reinforced the light microscopy observations. In mallow, mesophyll tissue from fresh leaves showed the typical cellular organization with chloroplasts aligned at cell periphery (Figure 3A) and retaining their normal ultrastructure, with well- preserved thylakoid membranes and grana (Figure 3B). In conventionally dried tissues, mesophyll cells appeared shrunken, with undulated cell walls; the cytoplasm and cell organelles were condensed together, mostly in cell center (Figure 3C). However, the most striking feature of these cells was the presence a huge number of plastoglobules in chloroplasts (Figure 3C and D), which mostly retained their shape, although swollen and with membrane interruptions but with thylakoid structure still visible (Figure 3E). Plastoglobules in chloroplasts were already described in senescent leaves of different species (Ghosh et al. 2001; Rasera et al. 2019) and a relationship between their production and response to abiotic and biotic stresses were reported (Bréhélin et al. 2007). Instead, mallow leaf samples dried at 20 °C showed a very different ultrastructure (Figure 3F and G). Mesophyll cells appeared less shrunken, but severely plasmolyzed; the dense protoplasm, retracted from cell wall, suggests a rapid cell death with organelle disintegration, though the high electron-density indicates that most of the cell content has been retained. Contrary to conventional desiccation, chloroplasts were hardly recognizable and plastoglobules possibly coalesced in large round bodies. Overall, from these observations it seems that cold drying apparently damages the leaf tissue structure more than conventional drying but somehow allows to retain most of the cellular content and in particular of chloroplast membrane lipids that seem to coalesce together in large dense round bodies. Instead, in conventionally dried samples at 40 °C chloroplasts, though preserving some thylakoid membranes, seems to lose most of the stroma and membrane lipids, which initially aggregate in numerous plastoglobules that are then released and possibly dispersed. It can be hypothesized that the 72 hours it took to cold dry the mallow samples (as opposed to the 48 hours it took for the other three herbs) affected the cellular anatomy more significantly.

As regards lemon balm leaves, their ultrastructure in samples fixed and embedded as soon as harvested, showed

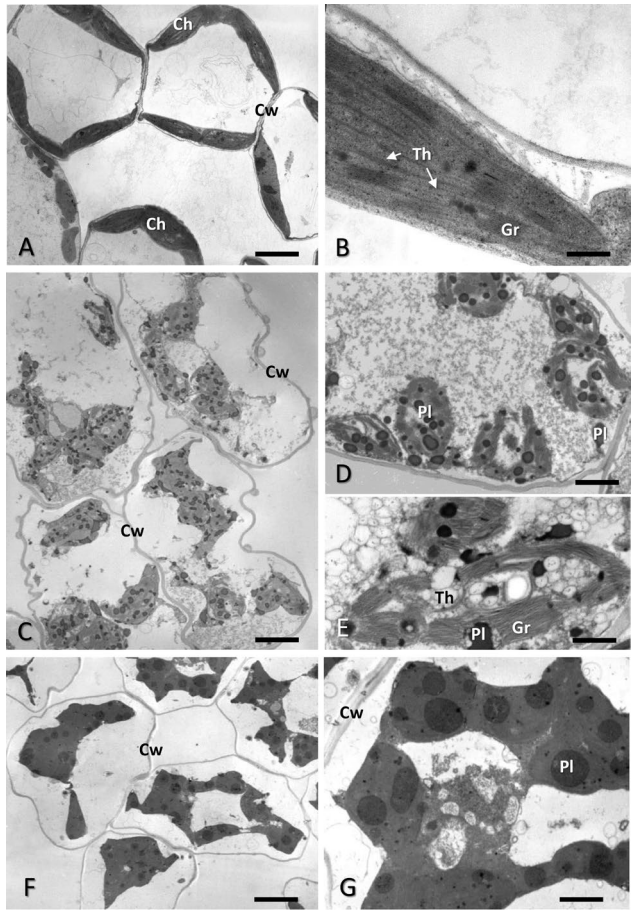

Figure 3. Ultrathin sections of *Malva sylvestris* L. mesophyll leaf tissue from fresh (A and B), conventionally dried (C–E) and cold dried (F and G) samples. A. Fresh leaves with typical cellular organization and chloroplasts aligned at cell periphery and showing well-preserved thylakoid membranes and grana (enlarged in B). C. Shrunken mesophyll cells of conventionally dried tissues with undulated cell walls; cytoplasm and cell organelles are condensed together, mostly in the center of cells; deranged chloroplasts contain numerous plastoglobules, sometimes released in the cytoplasm (D), however retaining their shape with thylakoid structure and grana still visible (enlarged in E). F. Leaf samples dried at 20 °C showing mesophyll cells severely plasmolyzed with a dense protoplasm retracted from cell wall, indicating a rapid cell death with organelle disintegration; chloroplasts are hardly recognizable and plastoglobules possibly coalesce in large round bodies (G). Ch = chloroplast; Cw = cell walls; Gr = grana; Pl = plastoglobules; Th = thylakoids. Bars = 4 µm in A; 0.4 µm in B; 3.7 µm in C; 1.7 µm in D; 1.1 µm in E; 2.2 µm in F; 2 µm in G.

mesophyll cells with a thicker layer of cytoplasm in respect to mallow, and consequently, the volume of vacuoles slightly reduced (Figure 4A–C). Moreover, in this species chloroplasts were less elongated and with a typical bean shape, and large nuclei were often visible in the cells, even in stomatal guard cells (Figure 4A–C). In conventionally dried leaves mesophyll cells appeared slightly distorted with chloroplast retracted by cell wall, however maintaining in most cases their peripheral position (Figure 4D). They appeared also very electrondense, sometimes distorted, and no thylakoid membranes, grana and plastoglobule were appreciable, except for a few exception (Figure 4F). Another peculiar feature of these dried samples was the presence of small empty vesicles of different size and possibly originated by degeneration of cell membranes. These vesicles were present also in stomatal guard cell (Figure 4E), in which the protoplasm was not preserved. The break-up of the single original

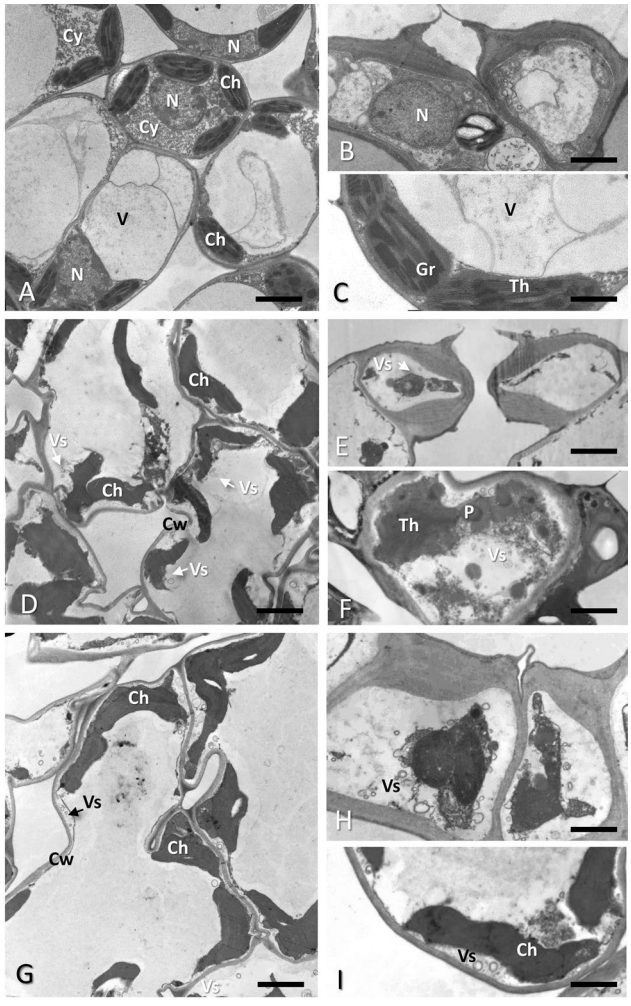

Figure 4. Ultrathin sections of *Melissa officinalis* L. mesophyll leaf tissue from fresh (A–C), conventionally dried (C–E) and cold dried (F and G) samples. A. Fresh leaves showing mesophyll cells with many nuclei, elliptical chloroplasts (enlarged in C) and abundant cytoplasm surrounding vacuoles; large nuclei were often visible in stomatal guard cells (B). D. In conventionally dried leaves mesophyll cells appear slightly distorted with chloroplast very electrondense; no thylakoid membranes, grana and plastoglobule are appreciable, except for a few exceptions (F); small empty vesicles of different sizes are visible in every cell, including the almost empty stomata cells (E). G. Leaves dried at 20 °C showing a very similar structure of those dried at 40 °C (D), with distorted and electrondense chloroplasts (I), very often retaining their peripheral localization, and the presence of numerous empty vesicles also in stomatal cells (H). Ch = chloroplast; Cw = cell wall; Cy = cytoplasm; Gr = grana; N = nuclei; Pl = plastoglobules; Th = thylakoids; VS = vesicles. Bars = 2 µm in A, B, D and E; 1.5 µm in C and H; 1.7 µm in F; 2.2 µm in G; 1 µm in I.

vacuole in numerous vesicular fractions is in agreement with previous observations of dehydrated leaf cells. This phenomenon was reported in several desiccation tolerant species as one of the cellular mechanisms of adaptation to drying (Quartacci et al. 1997). Lemon balm leaves dried at 20 °C showed a very similar structure of those dried at 40 °C, with distorted and electrondense chloroplasts, usually retaining their peripheral localization, and the presence of empty vesicles (Figure 4G–I). Thus, it seems that exsiccation of this species with the two methods leads to the same ultrastructural changes. A possible explanation could reside in the apparent compactness of lemon balm tissues, with cells rich in protoplasm and with reduced vacuole areas, that allow a less drastic drying and the retention of most of cell content, even though compressed in almost amorphous very dense structures.

Fresh mint leaves were characterized by roundish dark bodies, mostly at the cell periphery all through parenchyma tissues (Figure 5). These dark bodies, closely resembling polyphenols aggregates (Stefanowska et al. 2002) disappeared after both cold and conventional drying (Figure 4). This phenomenon was also observed in winter oilseed rape leaves subjected to low temperature, where large phenolic aggregates disappeared (Stefanowska et al. 2002). Indeed, the two drying systems gave similar results, with severe distortion of cell walls and the retraction of chloroplasts from them, although these organelles retained their peripheral localization. Another striking feature of mint leaf samples dried with both methods was the presence of amorphous large bodies, usually at the cell center and resembling in consistency the oil bodies typical of mint trichomes (Maffei et al. 2006). In spite of the apparent similarity of samples processed at 20 °C and 40 °C, it was possible to appreciate a slight better preservation of cell organelles at the lower temperature. In fact, in some cells nuclei still retained chromatin structure (Figure 5F) and mitochondria their cristae (Figure 5G). Overall, these observations indicate that in the case of mint the cold drying may be relatively better in maintaining some cell structures, though both drying temperatures dramatically affected tissue organization.

Savory fresh leaf tissue organization was significantly different from that of the other considered species with a palisade mesophyll cell layers under the two epidermis and a spongy mesophyll layer between them (Figure 2, panel A). Moreover, cells showed very thin cell walls and chloroplasts were not aligned along the whole cell wall but grouped in restricted areas (Figure 6A), though with a typical ultrastructure (Figure 6B). After drying at both temperatures cells appeared distorted or even collapsed with chloroplasts condensed in the center or between the walls of collapsed cells (Figure 6C and D). Chloroplast structure was quite damaged as well, even though thylakoids were partially visible (Figure 6C and D). Undoubtedly, the thin cell walls of mesophyll parenchyma cells of this species may account for the dramatic alterations observed with both the drying methods used, even though collapsed tissues were more frequent at cold dry (Figure 3, panel C), suggesting a better preservation of this species when dried in shorter time at higher temperature.

Conclusions

Our results suggest that, through a different impact at cellular level (degradation/disaggregation *vs* collapsing), it is very difficult to determine which of the two considered methods would be better for preserving the quality features of the different plant species. In the cases of lemon balm and mint, no striking differences were observed in term of cellular damages, while in mallow and in savory, cold drying and traditional drying, respectively, seemed to be the less impactful treatment on cells and tissues. The fact that diverse

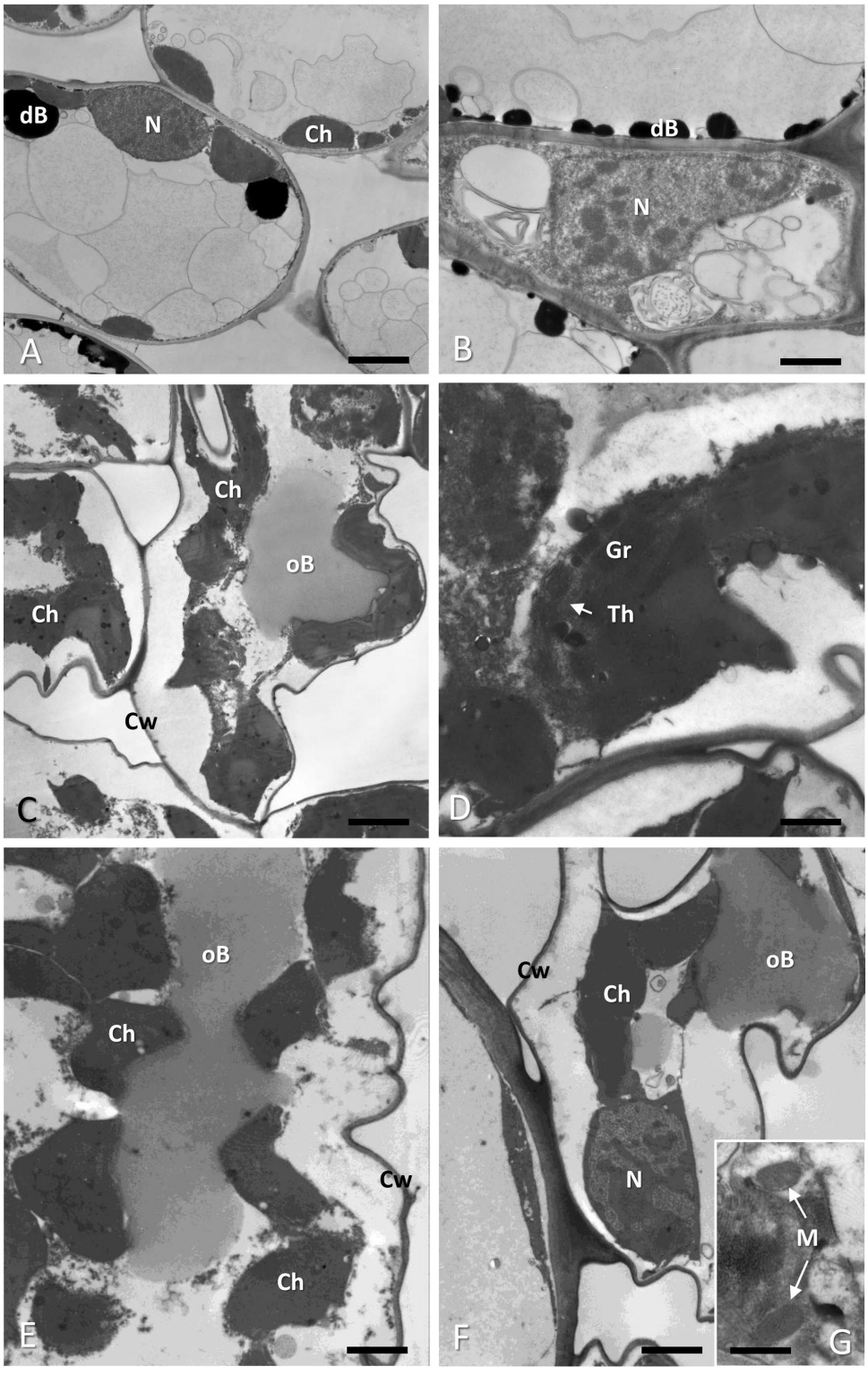

Figure 5. Ultrathin sections of *Mentha spp.* (mint) mesophyll leaf tissue from fresh (A and B), conventionally dried (C and D) and cold dried (F and G) samples. A. Fresh mint leaves showing a canonical ultrastructure, however with the presence of roundish dark bodies in mesophyll cells, mostly lined against cell walls (B). C. Dark bodies are not present after conventional drying; instead in these samples amorphous large bodies, resembling in consistency the oil bodies, are visible in the cell centre between dense and distorted chloroplasts, detached from cell wall, and showing only remnants of thylakoids and grana (enlarged in D). E. After cold drying the ultrastructure is similar as in C, with large bodies resembling oil bodies surrounded by dense and distorted chloroplasts, detached from cell wall. However, this method gives sometimes a slight better preservation of cell organelles as some cell nuclei still retain chromatin structure (G) and mitochondria their cristae (G). Ch = chloroplast; Cw = cell wall; dark bodies (dB); Gr = grana; M = mitochondria; N = nuclei; oil-like bodies (oB); Pl = plastoglobules; Th = thylakoids. Bars = 3.5 µm in A; 1.9 µm in B; 3 µm in C; 1 µm in D; 2.5 µm in E; 2 µm in F; 1.5 µm in G.

species respond differently to the two drying systems was in some way expected, as this depends on the anatomy and physiology of each species, with particular references to the tissue compactness, water content, cell wall thickness. In any case, and despite the small number of species investigated in this work, it should be underlined that the poor

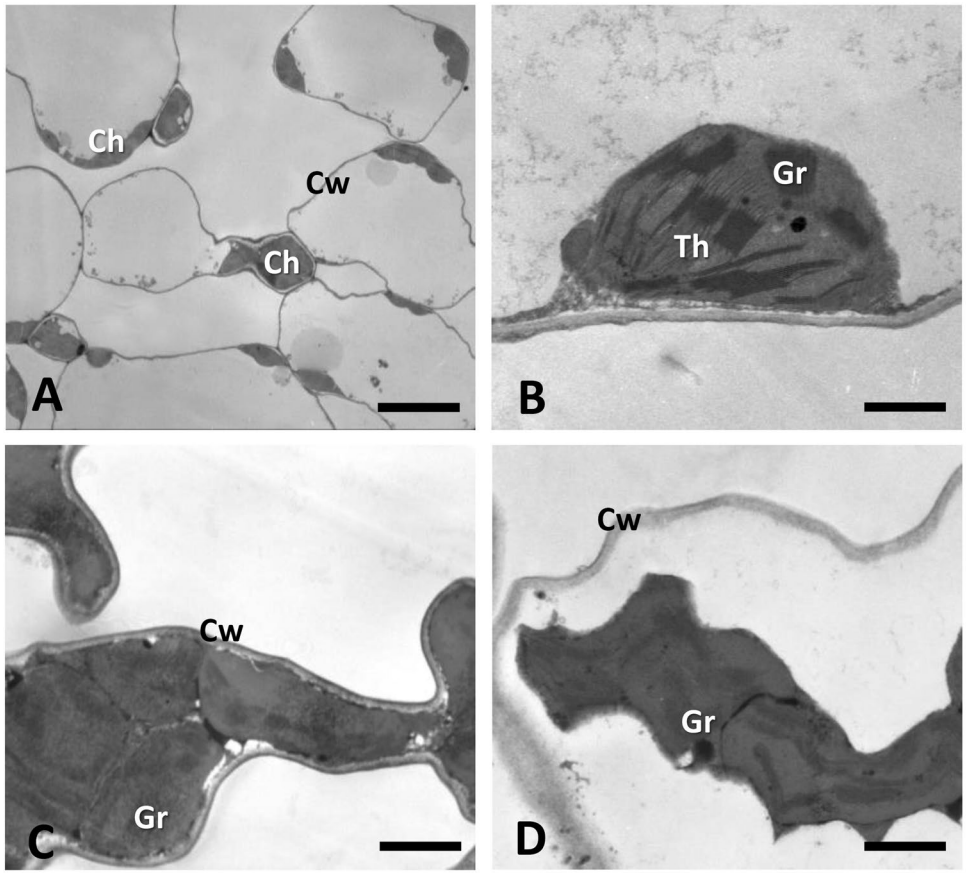

Figure 6. Ultrathin sections of *Satureja hortensis* L. mesophyll leaf tissue from fresh (A and B), conventionally dried (C) and cold dried (D) samples. A. In fresh leaf tissue, cells show very thin cell walls and chloroplasts grouped in restricted areas, however with a well preserved ultrastructure (enlarged in B). No significant differences are observed after drying at 40 °C (C) or 20 °C (D): in both samples cells appear distorted or even collapsed with chloroplasts condensed in the centre or between the walls of collapsed cells (C); some remnants of chloroplast grana are still visible in both dried samples (C and D). Ch = chloroplast; Cw = cell wall; Gr = grana; Th = thylakoids. Bars = 2.8 µm in A; 0.7 µm in B and C; 0.9 µm in D.

preservation of cellular structures was generally equal at either temperature drying or sometimes slightly better in drying at 20°. Therefore, considering that cold drying technology better preserved colour brightness and, more important, leads to approximately 30 to 70% higher electricity consumption, depending on the herb, compared to traditional drying, the choice should also concern these and other aspects. In particular, the preservation of aroma and in general the content of essential oil and bioactive compounds important for medical and culinary purposes should be evaluated for both drying technologies. This fundamental aspect will necessarily have to be investigated to reach a definitive conclusion.

Disclosure statement

No potential conflict of interest was reported by the authors.

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