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ORIGINAL RESEARCH

Saturated Aldehydes C6–C10 Emitted from Ashleaf Maple (*Acer negundo* L.) Leaves at Different Levels of Light Intensity, O_2, and CO_2

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Abstract Aldehydes, a group of volatile organic compounds (VOCs) often detected in the atmosphere, play a key role in atmospheric chemistry and plant resistance to stresses. We used gas chromatography/mass spectrometry to examine the volatiles of saturated aldehydes C6–C10 that were emitted from cuttings of ashleaf maple (*Acer negundo* L.) under varying levels of light intensity (80, 400, and 800 μmol m^{-2} s^{-1}), O_2 (2% and 50%), and CO_2 (600, 1,000, and 1,200 ppm). An apparent, positive correlation was found between light intensity and emissions, and their release also was significantly enhanced by higher O_2 concentrations. In contrast, emissions clearly were negatively correlated with CO_2 levels. We speculate that the reactive oxygen species (ROS) generated during photosynthesis contribute to these elevated emissions. However, the mechanism for this ROS trigger is unknown.

Keywords *Acer negundo* L. · CO_2 concentration · Light intensity · O_2 concentration · Reactive oxygen species (ROS) · Saturated aldehydes C6–C10

Oxygenated volatile organic compounds (VOCs) are important components that are often detected in the atmosphere. However, little is known about their sources. Plants are important emitters of a large number of oxygenated VOCs, e.g., alcohols, aldehydes, carboxylic acids, and terpenes (Kesselmeier and Staudt 1999; Peñuelas and Llusià 2001, 2004; Wildt et al. 2003; Staudt and Lhoutellier 2007). Among those measured from the atmosphere, short-chained aldehydes—such as hexanal (C6), heptanal (C7), octanal (C8), nonanal (C9), and decanal (C10)—have been found in concentrations from <10 ppt to >1 ppb. These aldehydes play a significant role in atmospheric chemistry and can be photolyzed by UV irradiation, leading to the formation of airborne radicals. Acetaldehyde and formaldehyde are involved in the production of tropospheric ozone and peroxyacetyl nitrates (PAN-family compounds), which adversely affect plant growth and human health (Graus et al. 2004). Because of their toxicity to insects, fungi, and bacteria, aldehydes are also used by plants as a defense against biotic stresses. Nandi and Fries (1976) have reported that pentanal, hexanal, and heptanal exhibit strong antifungal activities against several organisms, including two *Aspergillus* species in stored wheat seeds.

Aldehydes might be formed artificially when reactive species engage with organic compounds to form aerosols (Helmig et al. 1996), or when ozone interacts with adsorbants (Cao and Hewitt 1994). However, they have also been shown to be necessary volatiles emitted by plants (Ciccioli et al. 1993; Owen et al. 1997; Wildt et al. 2003). The release of hexanal (C6), an aldehyde in a group of green leafy volatiles (GLVs), has been well documented and found to act as a direct or indirect defense signal (Engelberth et al. 2004; Kishimoto et al. 2005). The emissions of 16 aldehydes, including 11 linear saturated aldehydes, three linear unsaturated, and two non-linear, are clearly enhanced by mechanical damage to the leaves of *Populus simonii* × *P. pyramidalis* 'Opera 8277' (Hu et al. 2008). Furthermore, emissions from the storage pools of plants, and production via a special biosynthesis pathway

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that requires the activity of an enzyme system, are possible mechanisms for these short-chain plant aldehydes (Wildt et al. 2003). For example, a lipoxygenase/hydroperoxide lyase (LOX/HPL) pathway leads to the formation of short-chain aldehydes C6- and C9- (Feussner and Wasternack 2003).

Volatiles in plants fluctuate diurnally and seasonally (Li et al. 2003; Mayrhofer et al. 2005; Pio et al. 2005), probably because of changes in temperature and solar radiation. Heat studies have indicated significantly increased emissions of VOCs exposed to high temperature (Lerdau et al. 1994, 1995; Constable et al. 1999). Emissions of aldehydes C6–C10 have been reported in sunflower, pine, corn, tomato, tobacco, and canola, again demonstrating that release of these compounds is enhanced by heat treatment (Wildt et al. 2003). Light, CO_2, and O_2 are environmental factors essential to plant growth and development. Light controls many important processes (Kraepiel et al. 2001), including the cell cycle (Symons and Reid 2003) and endogenous hormones (Suzuki and Kerbauy 2006). Plant volatiles are not emitted in the dark but their levels rise steadily as light intensity increases (Gouinguené and Turlings 2002). For example, enhanced light levels accelerate the release of C6-volatiles from *Lactuca sativa* L. plants (Charron et al. 1996). Loreto et al. (2006) have also found that high light causes increased emission of many VOCs, such as isoprene and acetaldehyde. However, the relationship between intensity and aldehyde emission is not completely understood. Because plants are exposed to varying light levels in the natural environment, this effect on volatiles emissions has important physiological and ecological significance.

Changes in atmospheric CO_2 concentrations also can affect plant physiology. Under elevated levels, plants are larger, grow faster, and have greater carbon:nitrogen ratios and smaller specific leaf areas (Bazzaz 1990; Poorter and Navas 2003; Sallas et al. 2003). The particular concentration of CO_2 also influences the emissions of volatiles, especially terpenoids. Depending on the plant species and individual compounds, terpenoid emissions are increased, decreased, or remain unaffected under elevated CO_2 (Constable et al. 1999; Loreto et al. 2001; Niinemets et al. 2004; Vuorinen et al. 2005; Himanen et al. 2009). However, the interaction of aldehydes with carbon dioxide is little known. Furthermore, because the concentration of atmospheric CO_2 is gradually rising, and is expected to double by the end of the twenty-first century, the effect on aldehyde emissions is becoming more and more obvious.

As a byproduct of photosynthesis, O_2 also influences leaf photosynthesis, resistances to CO_2 diffusion (Ludlow 1970), plant growth, lipid peroxidation, and receptivity of tomato roots to Pythium F (Chérif et al. 1997). A strong outburst of hexenal is also detected in Grey poplar [*Populus* × *Canescens* (Aiton) Smith] when O_2 is re-supplied under anoxic conditions (Graus et al. 2004). However, its influence on aldehyde emissions is large unknown.

Here, we used gas chromatography/mass spectrometry to examine the emissions of saturated aldehydes C6–C10 from ashleaf maple (*Acer negundo* L.), a common plantation tree species in China. Various levels of light intensity, O_2, and CO_2 were tested to monitor the response of woody plants to changes in environmental factors.

Materials and Methods

Plant Materials and Growing Conditions

Two-year-old cuttings of ashleaf maple (*A. negundo* L.) were grown in pots (25.0×25.0 cm) containing nursery top soil, all under a 16-h photoperiod and 25/20°C day/night cycle in the greenhouse of Beijing Forestry University. They were watered daily and supplied with a full Hoagland nutrient solution every 2 weeks to avoid water and nutrient stresses (Hu et al. 2004). Their volatiles were collected in July of 2007.

Light Treatment

Cuttings were exposed to one of three levels of light intensity—80, 400, and 800 μmol m^{-2} s^{-1}. A water curtain was interposed between their leaves and the light source to avoid heat damage from the Ds lamp. To acquire valid and consistent results, the cuttings were kept for 4 h at a particular light level before their volatiles were collected. CO_2 was supplied continuously to the bags to compensate for its consumption during photosynthesis. Each light treatment had three single-plant replications.

O_2 Treatment

Two levels of O_2—2% and 50%—were used to treat the maple cuttings, all at a light intensity of 400 μmol m^{-2} s^{-1}. Oxygen flow into the collection bag was controlled by a gas-flow meter to achieve the desired O_2 concentration. To obtain valid and consistent results, the plants were kept for 4 h at a particular O_2 level before their volatiles were collected. CO_2 was supplied continuously to compensate for its consumption during photosynthesis. Three single-plant replications were run for each O_2 treatment.

CO_2 Treatment

At 400 μmol m^{-2} s^{-1} light intensity and 20% O_2, we tested three levels of CO_2—600, 1,000, and 1,200 ppm. Pure CO_2 was injected into the collection bag to achieve the desired concentration. All cuttings were kept for 4 h under a particular

CO_2 level before volatiles were collected, and three single-plant replications were followed for each treatment.

Volatiles Collection

Reynolds™ oven bags (44.3×55.8 cm) were used because they release and absorb only a few volatiles. Samples of cuttings with similar leaf areas were placed in each bag. A glass tube (15.0×0.3 cm; Chrompack, Middelburg, the Netherlands) containing Tenax-TA (60 to 80 mesh, Chrompack) was the volatile trap in each bag, and we tried to prevent contact between the cuttings and that tube. A portable air sampler (QC-1; Beijing Municipal Institute of Labor Protection, China) served as the pump. The volatiles were collected for 1 h at a flow rate of 100 ml min^{-1} and a temperature of 26±2°C. Afterward, the glass tubes with the adsorbed volatiles were sealed and placed in a desiccator.

Volatiles Analysis

Using a gas chromatograph and mass spectrometer (Trace 2000-Voyager; Finnigan, Thermo-Quest, Rodano, Milan, Italy), we de-sorbed the volatiles by heating them in a CP-4010 TCT thermal desorption device (Chrompack) at 250°C for 10 min. We then cryo-focused them in a cold trap refrigerated by liquid N_2 to −100°C. This trap was then quickly heated to 260°C in 1 min to transport the volatiles into an analytical column (CP-Sil 5CB low-bleed, MS 60 m×0.32 mm i.d., and 0.5-μm film thickness). The column was programmed from 40°C to 270°C at 6°C min^{-1} and held for 10 min. Helium (20 kPa) was used as the propellant. The mass spectrometer was operated in a 70 eV EI ionization mode, and scanning was done from *m/z* 10 to *m/z* 400, for 0.4 s per scan.

Volatiles Identification and Quantification

Compounds were preliminarily identified by searching the NIST library in the data system of Xcalibur (Finnigan), and checked according to its retention index. To compare among the amounts of aldehydes released after different treatments, we used hexanal (C6) (Beijing Chemical Reagent Inc., China) as an external standard, as described previously (Ping et al. 2001a; Hu et al. 2008). After the hexanal was dissolved in ethanol, 1, 5, 10, or 50 μL of 1 mmol mL^{-1} dilutions were applied to cotton-tipped wooden dowels. These were then placed in a collection bag without plants, maintaining the same volume as when collecting volatiles from the cuttings. A characteristic ion intensity (E3) was used for further determining the amount of volatiles released (Ping et al. 2001b).

Results

Effect of Light Intensity on Emissions of Aldehydes C6–C10

Chromatographic profiles of our volatiles indicated that the five aldehydes, C6–C10, were emitted from ashleaf maple cuttings under all three levels of light, with a positive relationship existing between height of the peak and intensity (Figs. 1 and 2). The lowest amount of aldehyde released was for heptanal (C7; Fig. 2b), ranging from 2.2 E3 to 7.0 E3 when light intensity was raised from 80 to 800 μmol m^{-2} s^{-1}. Decanal (C10) had the greatest amount of emission, from 50 E3 to 110 E3 over that same range of intensities (Fig. 2e). All differences among emissions were significant ($P<0.05$).

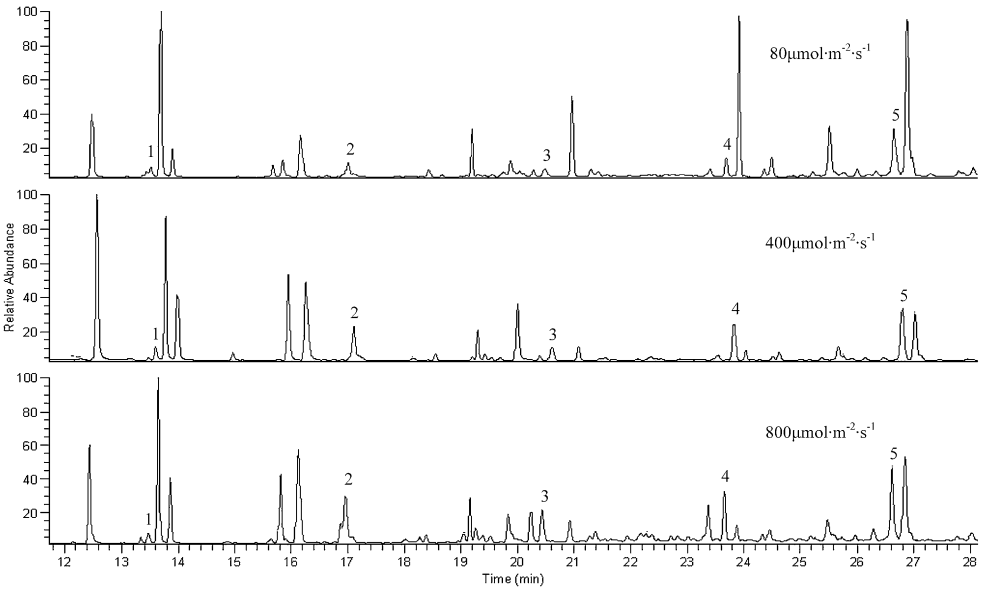

Fig. 1 Chromatographic profiles of volatiles from ashleaf maple cuttings at three light intensities (80, 400, and 800 μmol m^{-2} s^{-1}): *1* hexanal, *2* heptanal, *3* octanal, *4* nonanal, *5* decanal. Peaks for aldehydes C6–C10 show pattern of emissions increasing with elevated intensity. Volatiles detected by GC/MS were collected for 1 h at each intensity level (flow rate 100 ml min^{-1}). Chromatograms were performed at mass/charge ratio (*m/z*) of 41 as qualifier ion

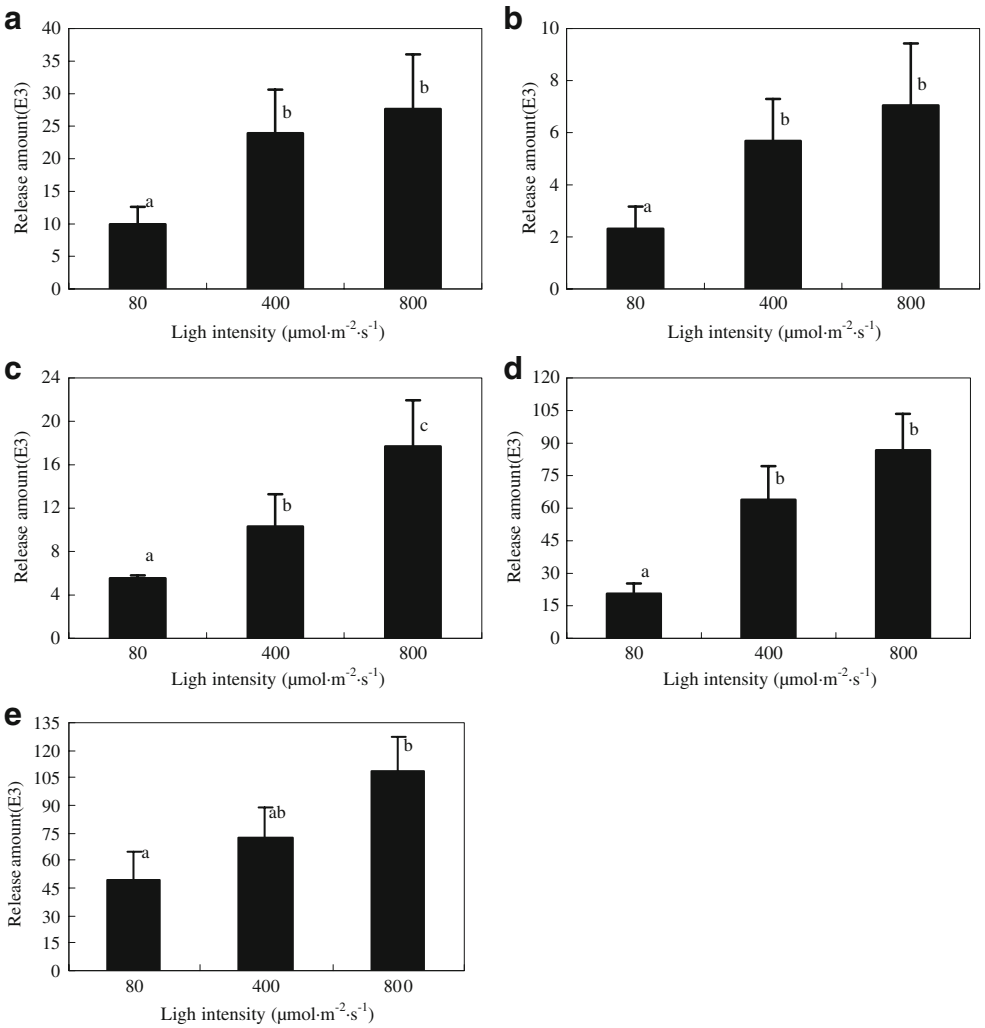

Fig. 2 Amounts of hexanal (**a**), heptanal (**b**), octanal (**c**), nonanal (**d**), and decanal (**e**) released from cuttings at three light intensities (80, 400, and 800 μmol m^{-2} s^{-1}). Each point is an average of three independent replications. Statistical significance [least significant difference (LSD) test, $P<0.05$] of differences among intensity levels is indicated by *lowercase letters*. Standard errors are shown

Amounts released were three- to fivefold higher at 800 μmol m^{-2} s^{-1} than at 80 μmol m^{-2} s^{-1}.

Effect of O_2 Concentration on Emissions of Aldehydes C6–C10

O_2 concentration had a marked effect on the emissions of all five aldehydes; at 2% O_2, their peaks were so low that they were hardly detectable whereas peaks were apparent at 50% O_2 (Fig. 3). Emissions were significantly larger ($P<0.05$) at 50% O_2 than at 2% O_2 (Fig. 4). For example, level of nonanal (C9) at 50% O_2 was about ten times higher than at 2% O_2 (Fig. 4d).

Effect of CO_2 Concentration on Emissions of Aldehydes C6–C10

We also tested the relationship between emissions and three levels of CO_2. Chromatographic profiles indicated that the amounts released gradually declined as concentration decreased (Figs. 5 and 6). Differences were statistically different for all three concentrations ($P<0.05$). For example, emissions of nonanal (Fig. 6d) and decanal (Fig. 6e) decreased about 20-fold when the level of CO_2 was increased from 600 ppm to 1,200 ppm.

Discussion

Although many oxygenated VOCs are found in the atmosphere, their sources are still debated. Some researchers have suggested that emission of aldehydes from biogenic sources is unlikely (Cao and Hewitt 1994; Helmig et al. 1996). However, other evidence implicates plants as an important source of aldehydes (Ciccioli et al. 1993; Owen et al. 1997). Here, we measured the release of five saturated aldehydes, C6–C10, from cuttings of ashleaf maple, thereby strongly supporting the hypothesis that aldehydes are emitted from biogenic sources.

Most previous studies have focused on aldehyde emissions and function under stress conditions. When plants are injured by herbivores or infected by pathogens, many

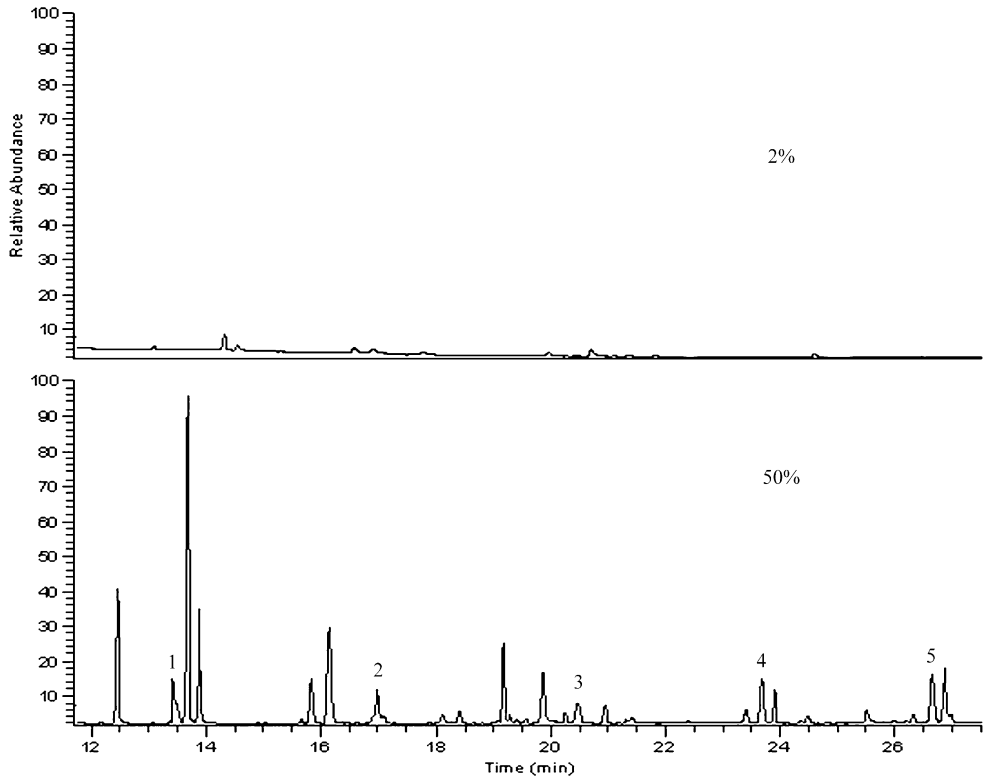

Fig. 3 Chromatographic profiles of volatiles from cuttings exposed to two O_2 concentrations (2% and 50%): *1* hexanal, *2* heptanal, *3* octanal, *4* nonanal, *5* decanal. Peaks for aldehydes C6–C10 are taller at high concentration than at low. Volatiles detected by GC/MS were collected for 1 h at each concentration (flow rate 100 ml min^{-1}). Chromatograms were performed at mass/charge ratio (*m*/*z*) of 41 as qualifier ion

aldehydes are formed and emitted (Thoma et al. 2003; Zeringue 1991). Wound-induced aldehydes show high resistance to insects and pathogens (Zeringue 1991). They also serve as airborne signals to attract natural, carnivorous enemies or induce a defense response in neighboring intact plants (Kishimoto et al. 2005). It was previously thought that plants not exposed to stresses emit only small amounts of aldehydes (Wildt et al. 2003). Graus et al. (2004) have found that light–dark transitions affect the release of acetaldehyde and aldehyde C6 in intact leaves of Grey poplar, suggesting an influence by light intensity. Plants treated with ozone exhibit higher emissions of aldehydes C6–C10 under high light than at low intensity (Wildt et al. 2003). Furthermore, acetaldehyde and (*E*)-2-hexenal are emitted in greater amounts from *Phragmites australis* leaves after exposure to high light and high temperature. This indicates that VOCs can be released by much larger tissue regions than just those that are wounded, and that even the fluctuations in light and temperature regularly observed in nature can induce emissions (Loreto et al. 2006). These reports demonstrate that environmental factors can affect aldehyde emissions. We also determined that emissions increased at greater light intensity. In response to treatment with O_2 and CO_2, the correlation was positive with the former but negative with the latter.

Possible explanations for these emissions in plants include release from their storage pools, or activity that follows production in a special biosynthesis pathway requiring an enzyme system (Wildt et al. 2003). Both mechanisms are possibly involved in the emissions of aldehydes C6–C10. Trace amounts of the aldehydes C6–C10 have been detected in poplar cuttings that are not stressed, indicating the likely existence of aldehyde pools (Hu et al. 2008). This process might be entirely of physical origin, and not dependent on light intensity. We believe that these pools also occur in ashleaf maple. Another mechanism—biosynthesis by enzymatic processes—is also a possible pathway for our five aldehydes. However, the increases in their emissions when plants were exposed to high light and O_2 imply that the enzymatic formation of those aldehydes requires the action of an enzyme system that could be regulated by any of these factors. Regulation is still unknown for the enzyme activity that is involved in the formation of aldehydes via light intensity or concentrations of O_2 and CO_2. Although a LOX/HPL pathway participates in the formation of short-chain aldehydes C6- and C9-

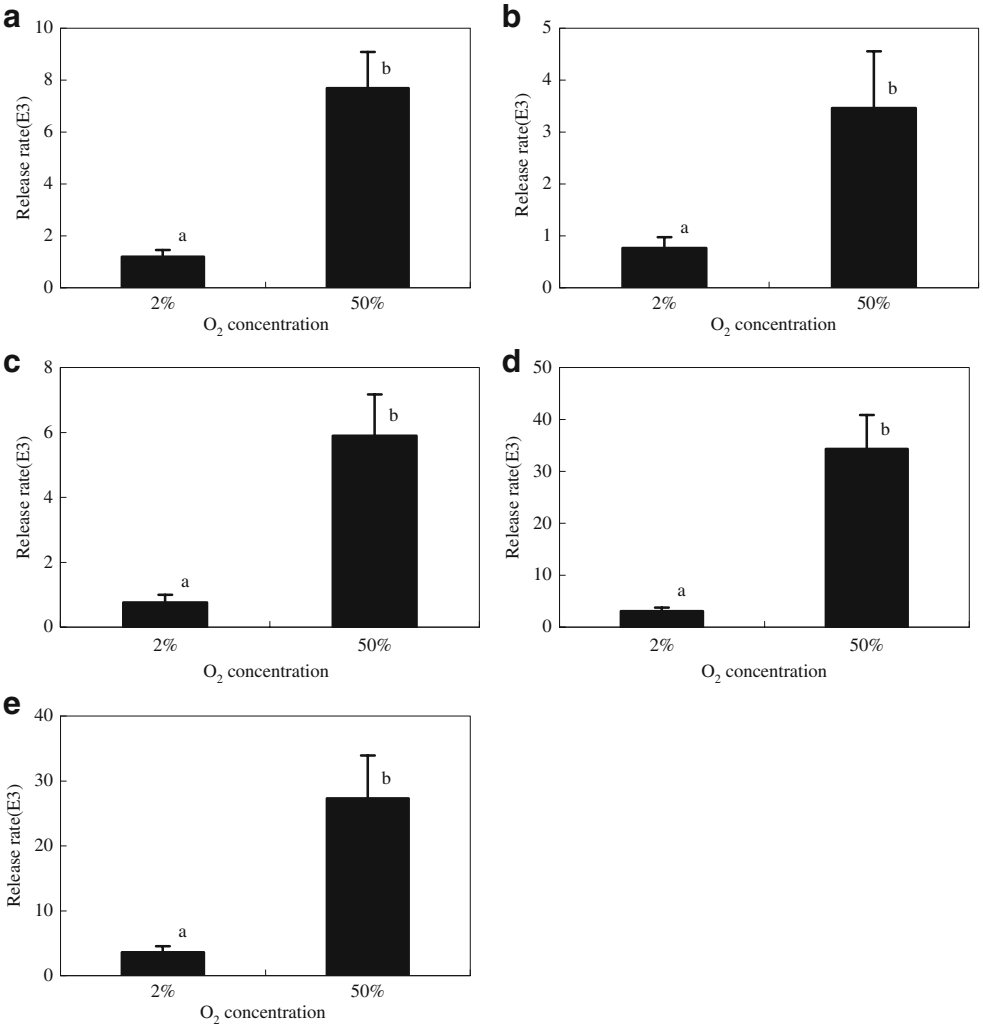

Fig. 4 Amounts of hexanal (**a**), heptanal (**b**), octanal (**c**), nonanal (**d**), and decanal (**e**) released from cuttings exposed to two O_2 concentrations (2% and 50%). Each point is an average of three independent replications. Statistical significance [least significant difference (LSD) test, $P< 0.05$] of differences among concentration levels is indicated by *lowercase letters*. Standard errors are shown

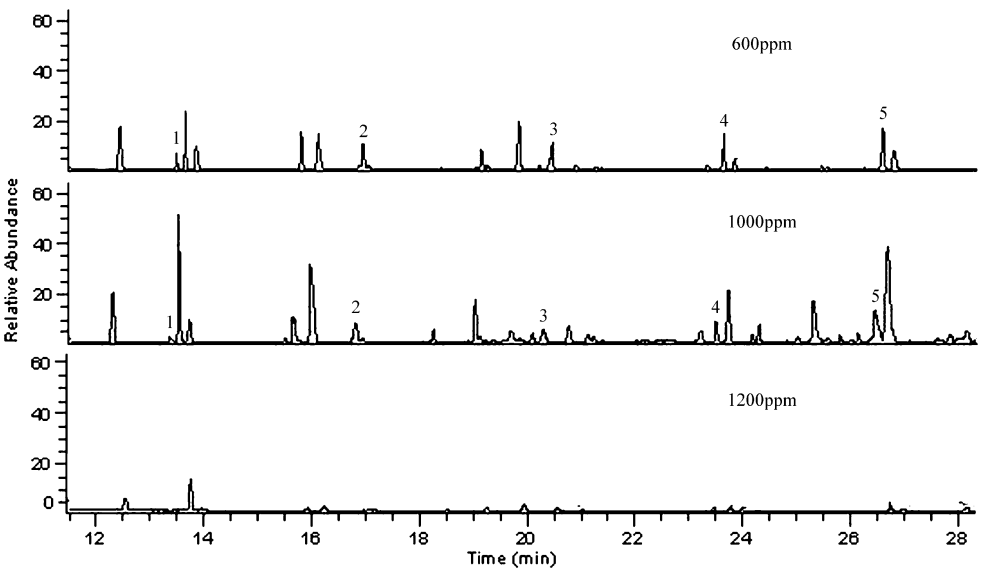

Fig. 5 Chromatographic profiles of volatiles from cuttings exposed to three CO_2 concentrations (600, 1,000, and 1,200 ppm): *1* hexanal, *2* heptanal, *3* octanal, *4* nonanal, *5* decanal. Volatiles detected by GC/MS were collected for 1 h at each concentration (flow rate, 100 mL min^{-1}). Chromatograms were performed at mass/charge ratio (*m*/*z*) of 41 as qualifier ion

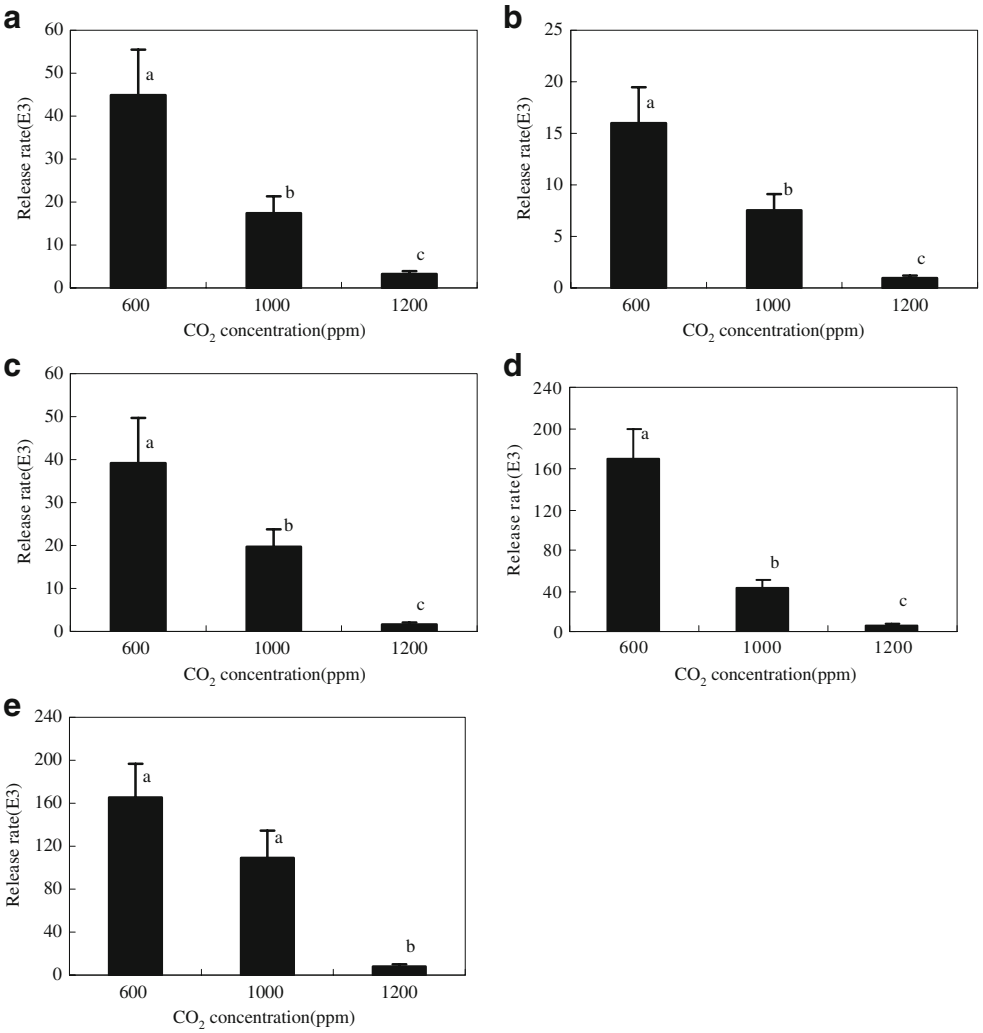

Fig. 6 Amounts of hexanal (**a**), heptanal (**b**) octanal (**c**), nonanal (**d**), and decanal (**e**) released from cuttings at three CO_2 concentrations (600, 800, and 1200 ppm). Each point is an average of three independent replications. Statistical significance [least significant difference (LSD) test, $P<0.05$] of differences among concentration levels is indicated by *lowercase letters*. Standard errors are shown

(Feussner and Wasternack 2003), it remains to be examined whether this enzyme system mediates the biosynthesis of other short-chain aldehydes, such as those investigated here.

In plants, photosynthesis in the chloroplasts is one of the most important physiological and biochemical processes, being closely related to light intensity, CO_2 level, and O_2 concentration. Therefore, we speculate that photosynthesis helps determine the amounts of aldehydes released under fluctuating environmental levels. Accumulations of ROS possibly contribute to aldehyde emissions from plants in response to biotic stresses (Wojtasek 1997), and those ROS may also have played a role in our study. Chloroplasts are the main site of ROS generation, such that photosynthesis is an important pathway (Kuang 2003). This provides strong support for its role in controlling the emissions of aldehydes C6–C10.

Molecular oxygen, a component of pseudocyclic electron transport in algae and higher plants, can be reduced to H_2O_2 via the Mehler reaction. This process is activated in higher plants when conditions are not advantageous for normal CO_2 fixation (Marsho et al. 1979). High light intensity and an elevated O_2 concentration can cause oxygen-free radicals to accumulate (Salin 1988). Using a histochemical localization technique, we found that increased levels of light and O_2 resulted in greater formation and accumulation of H_2O_2 and O_2^- in our ashleaf maple leaves (data not shown). Li et al. (2001) also have reported that ROS levels in the chloroplasts of four woody species—*Schima superba*, *Castanopsis fissa*, *Psychotria rubra*, and *Ardisia quinquegona*—regularly rise after light intensity increases. Our results also demonstrated a similar pattern of change between aldehyde emissions and ROS activity under varying light intensities and O_2 concentrations.

Based on these findings, we can infer that if CO_2 is sufficient, adding even more CO_2 will reduce the chance of O_2 being reduced to ROS. This ensures normal electron transport and fewer ROS being generated at high CO_2 concentration. Likewise, if formation of our five aldehydes truly is related to ROS, their release should show a negative relationship with CO_2 concentrations. Data from our current experiment provide strong support for this hypothesis of a negative correlation. Emissions were significantly lower at

greater CO_2 concentrations. Thus, ROS generated in the electron transport chain of photosynthesis might play a key role in the formation of aldehydes C6–C10.

In summary, five short-chain aldehydes were emitted from ashleaf maple cuttings that had not been exposed to pathogen infection or insect feeding. These emissions were clearly stimulated by increased light intensities and O_2 concentrations, but were negatively associated with CO_2 concentrations, which are involved with ROS generated in photosynthesis. Further research is needed to investigate the ROS-triggered mechanism for release of those aldehydes.

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