Chapter 10
Carbon Losses from Respiration and Emission of Volatile Organic Compounds—The Overlooked Side of Tree Carbon Budgets

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Abstract The balance between photosynthetic carbon (C) assimilation and C loss via respiration (R), emission of volatile organic compounds (VOCs), and rhizodeposition determines plant net primary production and controls to a large extent ecosystem C budgets. Compared to photosynthesis, the physiology, environmental control and ecological importance of processes involving C release from trees have been less studied; it is the purpose of this review to address these questions in oak trees with special focus on R and VOC emissions. Mass-based leaf dark R scales positively with specific leaf area, nitrogen content and photosynthetic capacity, and it is normally greater in deciduous species than evergreen sclerophyllous ones. Leaf dark R increases with temperature, and is constrained by water shortages; however, the magnitude of these responses may vary at different temporal scales. Similarly, R in woody tissues increases with temperature, although in a hysteretic manner during a diel period. On a seasonal basis, besides temperature, water availability becomes the main abiotic driver of woody tissue R as drought stress down-regulates maintenance and growth metabolic processes in stems and roots. Respiration in foliar and woody tissues is expected to account for about half of photosynthesis; nevertheless, R can largely fluctuate with ontogenetic, biotic and abiotic factors independently of C uptake. Volatile organic compounds have multiple roles in plant-environment interactions and plant-plant signalling. Oak genus is one of the

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strongest emitter of isoprenoids, which are the most important VOCs released from plants. Most oak species release isoprene constitutively; however, several oak species distributed around the Mediterranean (mostly evergreen) do not produce isoprene, but alternatively emit monoterpenes or lack constitutive emissions of VOCs. The rate of emission of VOCs from leaves increases with leaf temperature and irradiance, being the derived C loss relative to photosynthesis about 1%, except during heat waves when this percentage may increase up to 5%. Emission of VOCs is constrained by drought-stress to a lesser extent than leaf photosynthesis, thus the relative C loss through VOCs also increases with drought severity. Overall, the hypothesis of homeostatic ratios between plant C gain and C loss, an artefact of our better understanding of photosynthesis in comparison to all these processes that encompass tree C loss, should be revisited to better understand C cycling in oaks and to better predict oak physiological performance under climate change scenarios.

10.1   Introduction

The advance in the understanding of our environment is largely driven by the development of suitable technologies to quantify and explain the subject of study. Research in plant carbon (C) cycling clearly illustrates how methodological feasibility has driven knowledge in a particular direction (Körner 2015): As leaves can be easily enclosed in sealed chambers and gas exchange measured with an array of sophisticated systems (Hunt 2003), research on leaf C assimilation has traditionally held a predominant role in studying tree C budgets to the detriment of C efflux from other tree organs. Atmospheric CO_2 is assimilated by plants through photosynthesis (P) and part of it is released back to the atmosphere and soil through respiration (R), emission of volatile organic compounds (VOCs) and rhizodeposition. The difference between C assimilation and C loss is known as net primary production (NPP) and represents the net gain of C to be invested in plant growth, maintenance, defence, reproduction or storage. Net primary production is a key output of dynamic global vegetation models to predict C exchange between terrestrial ecosystems and the atmosphere. Net primary production is commonly calculated as the difference between P and R (e.g. Waring et al. 1998; Luyssaert et al. 2007; Piao et al. 2010; Rambal et al. 2014):

$$NPP = P - R \qquad (10.1)$$

In this equation, P is a well-known process mechanistically described more than 35 years ago (Farquhar et al. 1980), whereas R is a comparatively understudied C flux, despite its predominant role in ecosystem C balance (Valentini et al. 2000; Amthor 2000). Moreover, VOCs and rhizodeposits are commonly ignored in this

conceptual framework despite evidence of a non-negligible contribution to tree C loss (Jones et al. 2004; Bracho-Nunez et al. 2013; Sindelarova et al. 2014). Equation (10.1) should be therefore further developed to integrate all C fluxes between the plant and its environment:

$$NPP = P - R - VOCs - rhizodeposits \tag{10.2}$$

The biological significance of processes involving C release for survival and regeneration is unquestionable. Briefly, the mitochondrial oxidation of C substrates in all plant living cells produces reducing power [e.g. NAD(P)H from NAD(P)$^{+}$], C skeleton intermediates, and usable energy (ATP) from ADP and inorganic phosphate to fulfil metabolic requirements. During the numerous reactions of mitochondrial respiration CO_2 is formed, a fraction of which is released to the atmosphere, and another recycled within chloroplasts. VOCs are organic chemicals emitted from all plant organs that play multiple roles in plant reproduction, plant protection, and plant-plant signalling; whereas rhizodeposits consist of a wide range of compounds involved in plant nutrition, plant defence, and signalling between plant roots and surrounding organisms of the rhizosphere.

The genus *Quercus* comprises more than 600 species including deciduous and evergreen trees and shrubs adapted to a broad range of environmental conditions, from semi-arid Mediterranean evergreen woodlands to sub-boreal, temperate and subtropical deciduous forests (Mabberley 2008). Due to its wide distribution in the Northern hemisphere, *Quercus* spp. are extensively surveyed in physiological research and constitute an excellent taxonomic group to study the variability in R and the emission of VOCs among different plant functional types and across environmental conditions. In this chapter we want to draw the attention to an important side of plant C budget that has largely been overlooked in oak species: the release of C from the plant to the environment. We will focus on R and VOCs emission due to the scarce literature on oak rhizodeposition. We aim at (i) explaining the variability in R and VOCs emission among different oak species, along gradients of environmental conditions, and at different temporal scales; (ii) highlighting the relative contribution of R and VOCs emission to oak C budgets; (iii) and summarizing information on the chemical typology, mechanisms of synthesis and release, and ecophysiological significance of VOCs among oak species.

10.2   Plant Respiration

Plant R consists on the mitochondrial oxidation of C substrates to produce usable energy, reducing power, and C skeleton intermediates with the consequent release of CO_2 as a reaction product. Plant R is commonly simplified by a single equation developed in the early 1970s, in which R is partitioned into growth and maintenance processes (McCree 1970; Thornley 1970):

$$R \ = \ R_G + \ R_M = \ g_R G \ + \ m_R W \tag{10.3}$$

where R is respiration rate (mol CO_2 s^{-1}), R_G and R_M are growth and maintenance respiration rates (mol CO_2 s^{-1}), G is growth rate (g new biomass s^{-1}), W is living biomass (g dry mass), g_R is growth respiration coefficient (mol CO_2 (g new biomass)$^{-1}$) and m_R is maintenance respiration coefficient (mol CO_2 (g dry biomass)$^{-1}$ s^{-1}). Despite the magnitude of R, ca. 35 to 80% of P (Amthor 2000), substantial improvements in the mechanistic understanding of respiration are still lacking since the early 1970s (Cannell and Thornley 2000; Amthor 2000; Thornley 2011). Respiratory processes continue to be simplified by the growth-and-maintenance-respiration paradigm, and we are far from understanding respiration at the same detail as we do for photosynthesis (Farquhar et al. 1980). Gifford (2003) stated that "*plant respiratory regulation is too complex for a mechanistic representation in current terrestrial productivity models for carbon accounting and global change research*". This idea seems to be tacitly accepted and given that the rates of enzymatic reactions involved in R are temperature-dependent, plant R is commonly estimated from a single equation derived from Arrhenius kinetics (Davidson et al. 2006):

$$R \ = \ R_b \times \ Q_{10}(T - T_b) \, /10 \tag{10.4}$$

 where R is the respiration rate at temperature T, R_b is the respiration rate at a basal temperature T_b, and Q_{10} is the relative increase in respiration rate corresponding to a 10 °C temperature rise. Hence dynamic global vegetation models often estimate plant R from temperature data—neglecting other biotic and abiotic regulators of plant R such as water availability, C and nutrient supply, and energy demand—to quantify C fluxes and pools at the global scale (Smith and Dukes 2013; Fatichi et al. 2014). Alternatively, R is sometimes assumed to be a constant fraction of P at the tree scale (Waring et al. 1998; Van Oijen et al. 2010). Nevertheless, there is growing evidence that C cycling is not uniquely driven by C assimilation ("source-driven"), but also by abiotic constraints to plant growth and cell maintenance processes ("sink-driven") (see Körner 2015 for a review), as recently observed in *Q. ilex* (Lempereur et al. 2015), which challenges the assumption of homeostatic R:P ratios. Consequently, we are unable to accurately estimate plant R at different temporal and spatial scales, and to comprehensively understand the regulation of the plant respiratory physiology despite its primary role in tree C cycling, productivity and survival (Atkin and Macherel 2009).

   In this section, we distinguish between leaf and woody tissues to better summarize current knowledge on oak R. The physiological functioning of an organ is determined by its particular anatomy and structure, and thus leaves and woody tissues have different energy requirements and C-related expenditures derived from respiratory processes. Moreover, dissimilar methodological approaches to quantify R in different organs have contributed to further distance R research between leaves and woody tissues.

10.2.1 Leaf Respiration

10.2.1.1 Physiology and Variability Among Species

Leaf R is mostly dependent on the availability of ADP, C substrates—lipids, amino acids and mostly carbohydrates—and the amount, position and protein content of mitochondria within leaf cells, particularly mesophyll cells, whose contribution to total leaf R in some species is >90% (Long et al. 2015). Data compilations from plant species across the globe evidence that mass-based leaf dark respiration (R_d) rates—more easily measured and typically higher than leaf R rates in light conditions (Zaragoza-Castells et al. 2007)—are positively related with specific leaf area (SLA), leaf nitrogen (N) concentration and photosynthetic capacity (P_{max}) (Reich et al. 1998; Wright et al. 2006; Reich et al. 2008; Atkin et al. 2015). In the first case, the relationship is due to the lower proportion of structural components in high-SLA leaves; in the second, to the higher amount of respiratory enzymes present in leaves with high N concentrations. Finally, the correlation of R_d with P_{max} can reflect the role of P_{max} in providing the mitochondria with respiratory C substrates, or the importance of N for synthesizing both respiratory and photosynthetic enzymes.

Because oak species encompass a wide gradient of leaf functional characteristics, primarily abridged in the separation of broad-leaf evergreen and deciduous oaks, variability in leaf R_d rates among oak species is also large and partly related with climate conditions. Taking as example the 13 oak species included in the global database of respiration GlobResp (Kattge et al. 2011; Atkin et al. 2015), both area- and mass-based leaf R_d varied by approximately sevenfold. Global patterns across broad climatic gradients evidence that plant species from cold sites exhibit higher rates of leaf R_d than those from warmer sites at a comparable measurement temperature, a pattern that holds for oak species (Kattge et al. 2011; Atkin et al. 2015). Further, plant species from dry sites tend to have higher leaf R_d rates than those from mesic sites (Atkin et al. 2015), with this difference being only partly explained by differences in SLA or P_{max} (Wright et al. 2006). Some adaptations to stress, such as high rates of metabolite turnover can result in high respiratory costs in processes of cell maintenance and repair in cold, high-light or arid environments (Wright et al. 2006; Atkin et al. 2015). Similarly, high N investment in repair compounds could also explain why individuals from colder and drier populations of *Q. ilex* exhibited higher leaf maintenance respiratory costs than those from warmer and wetter populations when grown under the same conditions (Laureano et al. 2008). However, different evolutionary selection pressures, including abiotic and biotic stress factors and competition for resources have shaped the respiratory metabolism in different ways, which precludes a straightforward relationship of leaf R_d with stress resistance. As such, some leaf structural and chemical adaptations to stress, such as low N concentrations and low biomass allocation to metabolic components, can result in low leaf R_d rates in long-lived, sclerophyllous leaves of some oaks growing in nutrient-poor or drought-prone sites. At a comparable temperature of 25 °C, mass-based leaf R_d was lowest in
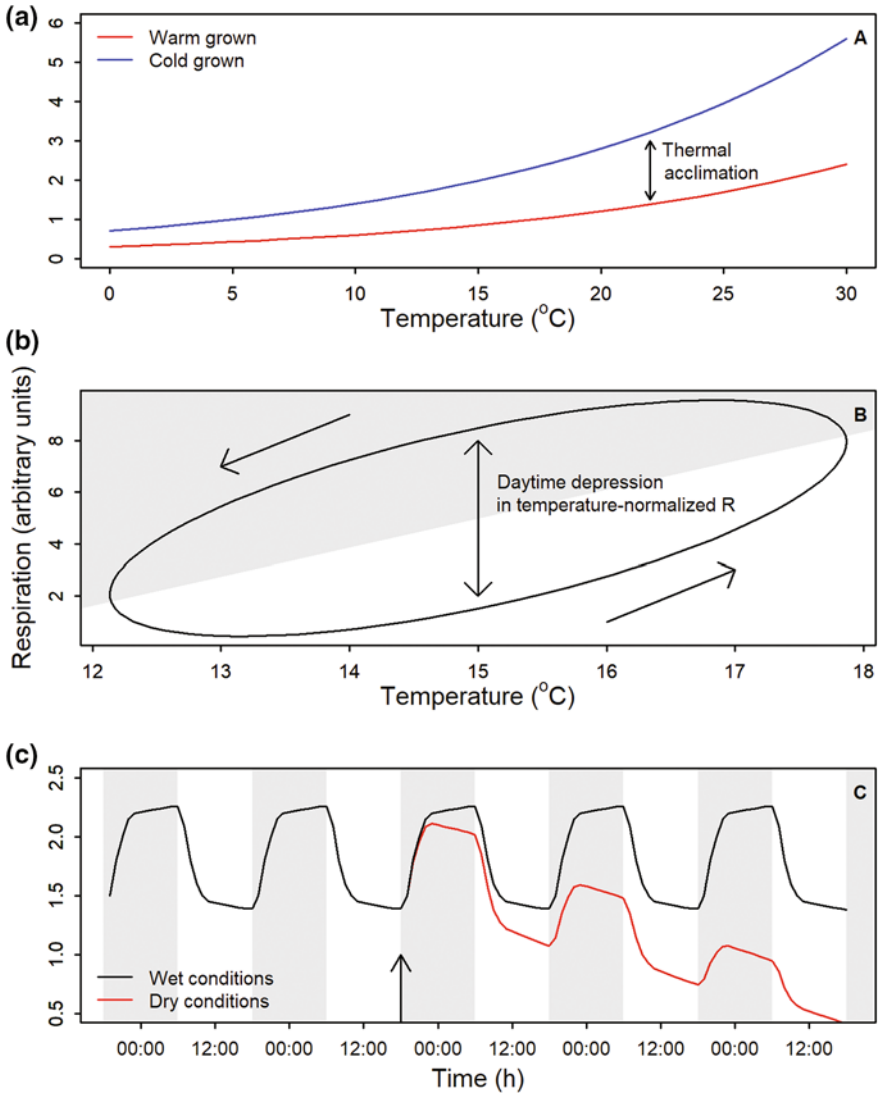
Fig. 10.1 Theoretical representation of the plant respiration (R) response to shifts in temperature (**a**, **b**) and water availability (**c**) at different temporal scales. Respiration exponentially increases with temperature at any temporal scale; however, thermal acclimation (commonly observed in leaves) leads to lower respiratory capacity of tissues grown under warm conditions (**a**, adapted from Atkin and Tjoelker 2003). Hysteresis between R and temperature over diel cycles has been observed for stem R, but not for leaf dark R (even if leaf R at a given temperature is usually lower in light than dark conditions) (**b**, adapted from Salomón et al. 2016b). Improved water status at night-time increases stem R under constant temperature on a diel basis, whereas stem R progressively decreases when water availability becomes limiting on a seasonal basis, as theoretically illustrated during the drought event (the beginning of the drought is represented by the vertical arrow) (**c**, adapted from Saveyn et al. 2007b). Shaded areas indicate night-time

the Mediterranean evergreen *Q. ilex* (4.0 nmol CO_2 g^{-1} s^{-1}) and highest in the deciduous *Q. alba* and *Q. rubra* (25–27 nmol CO_2 g^{-1} s^{-1}). This is consistent with low P_{max} of sclerophyllous leaves, and the positive relationship between P_{max} and leaf R_d (Wright et al. 2006).

10.2.1.2 Response to Environmental Changes at Different Time Scales

Within species, R_d varies in relation to ontogeny and environmental changes. As oak leaves progressively stop growing, both in lamina area and thickness, R_d decreases rapidly and reaches a phase in which fluctuations are not due to ontogenetic changes but mostly to climatic shifts; eventually, when leaves start to senesce, R_d starts to decline again markedly due to remobilization of leaf N and degradation of the respiratory machinery (Collier and Thibodeau 1995; Miyazawa 1998; Xu and Baldocchi 2003; Rodríguez-Calcerrada et al. 2012). Ontogenetic variations over the leaf life span make that, for comparative purposes, measurements of R_d are typically made in non-senescent mature leaves that have fully expanded. However, the responses of leaf physiology and R_d to climatic shifts can vary as affected by ontogeny and age, something that clearly merits more research to improve C balance models (Niinemets 2014).

The plasticity of R_d to air temperature, irradiance or water and nutrient availability is considerable in oak species. Multiple changes occur in the respiratory metabolism in response to the need of the tree to adjust the production of respiratory products to shifting demands imposed by environmental changes. This plasticity in the respiratory metabolism—reflected in varying rates of R_d—allows trees to orchestrate whole-plant plasticity and overcome periods of sub-optimal growing conditions. Two of the most important drivers of leaf physiology over the leaf life span are temperature and water availability.

Changes in temperature elapsed over hours, days, months or years affect the rates of R_d. However, the magnitude of the change in R_d rates depends on the time scale of temperature changes. Short-term raises in temperature provoke an exponential increase in leaf R_d that is typically higher than that occurred over longer term warming periods due to the thermal acclimation of the respiratory metabolism (Reich et al. 2016). This process of acclimation involves a reversible decline in the activity of respiratory enzymes. Frequently, the respiratory capacity (i.e. intercepts of respiratory temperature response curves) differs across temporal scales, probably due to shifts in the amount of mitochondria or mitochondrial enzymes. The consequence of this is that R_d measured at prevailing ambient temperature barely changes over broad, long-term changes in temperature (see Fig. 10.1a for an illustration of this phenomenon, and Slot and Kitajima 2015 for a recent review of the process across biomes and experimental conditions). The thermal acclimation of leaf R (more easily and frequently examined in dark than light conditions, i.e. R_d) is a general response of healthy, non-growing oak leaves (e.g. Bolstad et al. 2003; Lee et al. 2005; Zaragoza-Castells et al. 2008; Rodríguez-Calcerrada et al. 2011) that may accompany different thermal photosynthetic adjustments to balance leaf net C gain with C needs in the new environment

(Way and Yamori 2014; Slot and Kitajima 2015). The extent of the thermal acclimation of R_d varies among species and with leaf developmental status, magnitude of temperature change (Slot and Kitajima 2015) and interaction with other abiotic factors such as irradiance (Bolstad et al. 1999) or soil water availability (Turnbull et al. 2001; Rodríguez-Calcerrada et al. 2011).

Despite the importance of C losses for leaf and plant C balance, very few studies have examined the impacts of temporal soil water fluctuations on R_d in oak species. Most of these studies have been conducted on the drought-tolerant, widespread Mediterranean oak *Q. ilex* (e.g. Rodríguez-Calcerrada et al. 2011; Varone and Gratani 2015). The results of these studies are consistent with the drought-induced decline in leaf R_d and increase in leaf R_d/P ratio that is generally reported for other plant species (see review of Atkin and Macherel 2009). The main reasons behind this short-term decline in leaf R_d are: (i) a reduction in the amount of mitochondrial protein and (ii) a reduction in enzymatic activity due to limited turnover of ATP to ADP (associated to down-regulation of energy consumption processes) or limited flow of triose phosphate from chloroplasts into mitochondria (associated to impaired P). The complex regulation of leaf R makes that, as it happens in response to temperature, leaf R_d does not necessarily exhibit the same response to drought over short- and long-term time scales. However, few studies have examined how long-term decreases in soil water availability affect leaf R and C balance in oak trees (Turnbull et al. 2001; Rodríguez-Calcerrada et al. 2011; Sperlich et al. 2016). In southwestern Europe, two parallel throughfall-reduction experiments have been set up in two *Q. ilex* forest stands to study the long-term effects of increased drought on foliar respiratory rates. Rodríguez-Calcerrada et al. (2011) observed that leaf R_d decreased in response to seasonal decline of leaf water potential similarly in trees subjected to normal and 7-year reduced throughfall, so that leaf R_d was lower in the trees that had experienced a reduction in throughfall and a greater decline of leaf water potential during the dry season, but did not differ between treatments at optimal soil water conditions. These results and those of Limousin et al. (2010) on the nature of photosynthetic limitations in the same species and experimental site suggested that 7 years of increased drought had not modified the physiology of leaf mesophyll cells. In another *Q. ilex* stand subjected to a longer period of rain reduction (14 years) of similar intensity, Sperlich et al. (2016) found the same lack of treatment effect on leaf R_d, but a significant increase in leaf R during daytime in trees receiving less rain, suggesting that the reorganization of the respiratory metabolism depends on the duration of increased drought. Collectively, the results suggest that drought-induced declines in leaf R over short time periods seemingly change to drought-induced increases in leaf R as trees adapt to increased drought (Turnbull et al. 2001; Rodríguez-Calcerrada et al. 2011; Atkin et al. 2015; Sperlich et al. 2016), however, more studies are needed to understand long-term responses of leaf R to drought.

10.2.2   Stem and Root Respiration

10.2.2.1   How to Estimate It? Methodological Constrains to Measure Woody Respiration

Although stems and roots constitute the largest fraction of biomass in woody species, especially in large trees (Poorter et al. 2012), our knowledge of woody R is by far less advanced compared with that of leaf R. The main obstacle to understand R in woody tissues remains in the difficulty to accurately measure it. Radial CO_2 efflux to the atmosphere (E_A) from stems and roots, which can be measured with cuvettes surrounding the monitored organ, is commonly assumed to equal the rate of R of these organs. Nevertheless, locally respired CO_2 in roots and stems can either diffuse to the soil or the atmosphere, respectively, or alternatively accumulate within woody tissues due to substantial barriers to radial gas diffusion offered by outer tissues. Accordingly, concentrations of internal CO_2 in xylem (xylem $[CO_2]$) range from <1 to 26%, values one to two orders of magnitude higher than atmospheric $[CO_2]$. As xylem $[CO_2]$ builds up inside the tree, it dissolves in the sap solution until equilibrium between gaseous and liquid phases is reached according to Henry´s law; respired CO_2 moves upward in the transpiration stream, and eventually diffuses to the soil or the atmosphere elsewhere (see Teskey et al. 2008; Rodríguez-Calcerrada et al. 2015b for reviews). Internal transport of respired CO_2 has therefore resulted in significant misestimation of woody R from measurements of E_A, as consistently observed in several oak species (McGuire and Teskey 2002; Teskey and McGuire 2002; Bloemen et al. 2014; Salomón et al. 2016b).

An additional constraint that hinders direct measurements of woody R is the re-assimilation of internal CO_2 by chloroplast-containing woody tissues (see Ávila et al. 2014 for a review). For instance, recycling of respired CO_2 transported through the xylem offset 19 and 70% of C respiratory losses in branches of *Q. alba* and stems of *Q. robur,* respectively (Coe and McLaughlin 1980; Berveiller et al. 2007). To solve this issue, woody P is commonly disabled by using opaque cuvettes; nevertheless, woody P above and below the cuvette might induce axial diffusion of internal CO_2 that would decrease E_A within the monitored segment, as observed in *Q. robur* stems during the dormant season (Saveyn et al. 2008). Additional difficulties arise when measuring root R due to inaccessibility of root systems and the unclear discrimination between autotrophic and heterotrophic respiration from measurements of soil CO_2 efflux (Hanson et al. 2000). All these limitations hinder the establishment of a widely accepted methodological approach to systematically measure woody R.

10.2.2.2   Response to Environmental Changes at Different Time Scales

Due to the few studies on woody R in oaks, the influence of abiotic drivers (mainly temperature and water availability) on woody R is summarized independently of

any intrageneric classification. In a study with seven oak species grown under uniform conditions, Martinez et al. (2002) did not find any intrinsic difference in root R attributable to the evergreen or deciduous character of the species. Likewise, potential differences in woody R ascribed to the ring-porous or diffuse-porous wood anatomy of oaks remain untested, despite their differential wood phenology and growth (Pérez-de-Lis et al. 2016).

The temperature sensitivity of woody R, expressed as the change in R that occurs over 10 °C (Q_{10}) ranges from 1.4 to 3.1 in oak species, with mean values close to two (i.e., R rates double for an increase in temperature of 10 °C, Table 10.1), as similarly observed for a variety of species in leaves and roots (see Atkin and Tjoelker 2003 and references therein). On a diel basis, woody R increases along the day with increasing temperatures and decreases at night-time exhibiting a characteristic hysteresis (Table 10.1; Fig. 10.1b). Several factors have been suggested to cause the day-time depression in temperature-normalized stem R observed in oaks: (i) internal transport of respired CO_2 with the transpiration stream at day-time (Negisi 1982; McGuire and Teskey 2002; Teskey et al. 2008), (ii) enhanced metabolic activity of woody tissues owing to improved water status at night-time (Negisi 1982; Saveyn et al. 2007a; Salomón et al. 2016b), (iii) lagged temperature transmission and/or delayed radial CO_2 diffusion due to physical barriers presented by peripheral tissues (Rodríguez-Calcerrada et al. 2014), and (iv) refixation of respired CO_2 nearby the darkened monitored stem segment at day-time (Saveyn et al. 2008). At a seasonal scale, the down-regulation of temperature-normalized R with increasing temperatures across the year (Atkin and Tjoelker 2003) has the potential to reduce C loss through woody R. The thermal acclimation of leaf R (Fig. 10.1a) is a well-documented phenomenon in oaks (see previous sub-section) that has been less studied in woody tissues. A meta-analysis across 44 forested ecosystems, six of them dominated by oak species, supports the hypothesis of thermal acclimation of R in roots (Burton et al. 2008): An attenuated rate of temperature-driven increase in root R across ecosystems ($Q_{10} = 1.6$) was observed in comparison to short-term fluctuations within individual stands ($Q_{10} = 2$–3). Likewise, lower rates of temperature-normalized root R were registered in experimentally heated plots in mixed hardwood forests co-dominated by *Q. velutina*, although the concomitant effect of soil drying along with soil heating could not be discarded as a driver of R reductions (Burton et al. 2008). Thermal acclimation of R rates in stems may also occur in oak species such as *Q. ilex* (Rodríguez-Calcerrada et al. 2014), but literature is much scarcer in this regard. Again, the concomitant increase in temperature with summer drought in some ecosystems hinders to unequivocally ascribe seasonal reductions in stem R to thermal acclimation, given that water shortages constrain stem growth and associated respiratory costs in this widespread Mediterranean oak (Lempereur et al. 2015). The different temperature sensitivity of metabolic processes involved in maintenance and growth R (Amthor 2000) complicates the study of acclimation of maintenance R to abiotic stress in sites where secondary growth varies amply throughout the year. Accordingly, higher Q_{10} values observed in stems of *Q. accutisima* during the colder non-growing season relative to the warmer growing

Table 10.1 Temperature sensitivity of stem and root respiration (Q_{10}) in *Quercus* species

Organ	Species	Q_{10}	Hysteresis[a]	References
Stem	*Q. accutisima*	2.2		Yang et al. (2012b)
	Q. alba	1.5–2.4	✓	Edwards and Hanson (1996), Li et al. (2012)
	Q. ilex	1.5–2.5	✓	Rodríguez-Calcerrada et al. (2014)
	Q. mongolica	2.1–2.4		Wang et al. (2010), Yang et al. (2012a)
	Q. petraea	1.6 2.1		Rodríguez-Calcerrada et al. (2015a)
	Q. prinus	2.4	✓	Edwards and Hanson (1996)
	Q. pyrenaica	1.4–2	✓	Rodríguez-Calcerrada et al. (2015a), Salomón et al. (2016b)
	Q. *robur*	1.9–2.8	✓	Saveyn et al. (2007a, b, 2008)
	Q. serrata	2.1	✓	Miyama et al. (2006)
	Q. velutina	1.6		Li et al. (2012)
Roots[b]	*Q. accutisima*	2.8		Luan et al. (2011)
	Q. serrata mixed stand	2.4		Dannoura et al. (2006)
	Q. cerris	2.2		Rey et al. (2002)
	Quercus-Carya stand	3.1		Burton et al. (2002)
	Mixed *Quercus* stand	2.4		Burton et al. (2002)

[a]Studies in which a hysteretic relationship between temperature and respiration has been reported (✓). Empty spaces denote studies in which this phenomenon was not evaluated. [b]Root respiration integrates CO_2 originated from fine and coarse roots as well as root-associated microorganisms present in the rhizosphere

season were attributed to the greater temperature sensitivity of maintenance processes (Yang et al. 2012b) rather than to the potential effect of thermal acclimation of R.

Oak species subjected to drought stress commonly show reduced R as a consequence of constrained growth and metabolic activity. This effect has been observed at the ecosystem (Reichstein et al. 2002; Unger et al. 2009; Rambal et al. 2014), organ (Saveyn et al. 2007b; Rodríguez-Calcerrada et al. 2014), and cellular level (Saveyn et al. 2007a). During a diel cycle, night-time reduction in the vapour pressure deficit and transpiration lead to replenishment of water reservoirs within woody tissues (Steppe et al. 2006), as observed in *Q. ilex* (Salomón et al. 2017). Increase in cell turgor facilitates cell expansion and growth (Lockhart 1965), which in turn may lead to enhanced rates of overall R. This hypothesis of growth respiration mainly confined to night-time hours is supported by substantial night-time increases in both E_A and xylem [CO_2] observed in *Q. robur* stems under relatively

constant temperature across 24 h (Fig. 10.1c; Saveyn et al. 2007a, b). During the course of a year, progressive soil drying in summer was found to constrain fine root turnover (López et al. 2001) and stem growth (Lempereur et al. 2015) in *Q. ilex*. Impeded growth and down-regulation of maintenance processes likely explains typical reductions in woody R when water becomes limiting (Fig. 10.1c), as observed in roots of *Q. cerris* (Rey et al. 2002), *Q. robur* (Molchanov 2009), and mixed oak stands (Burton et al. 2002), as well as in stems of *Q. ilex* (Rodríguez-Calcerrada et al. 2014) and *Q. robur* (Saveyn et al. 2007b). Drought-induced reductions in R suggest a threshold in soil water content below which woody R becomes largely driven by water availability and independent of temperature (e.g. Reichstein et al. 2002; Rey et al. 2002). Likewise, sharp increases in xylem $[CO_2]$ observed in *Q. robur* and *Q. pyrenaica* stems after rain events following dry periods (Saveyn et al. 2007b; Salomón et al. 2016a) provide further evidence of drought-driven constraints to woody R. On the other hand, reduced resistance to radial CO_2 diffusion due to reduced water content of peripheral woody tissues as the soil dries out (Teskey et al. 2008; Salomón et al. 2016b) may partially explain increases in stem and root CO_2 efflux during mild drought in oak trees (e.g. Edwards and Hanson 1996; Dannoura et al. 2006; Molchanov 2009). Such conflicting results evidence our deficient understanding of drought effects on woody R. At an inter-annual timescale, acclimation of stem R to long-term increased drought was not observed in *Q. ilex* after eight years of experimental throughfall-reduction (Rodríguez-Calcerrada et al. 2014). Further research in this line would be necessary to test potential down-regulation of woody R to prolonged drought in order to better predict C cycling at the whole-tree level under changing climate regimes.

10.2.3 Relative Importance of R for Tree Carbon Budgets

Ecosystem R (R_{ECO}) determines ecosystem C balance in a wide range of environmental conditions (Valentini et al. 2000). Ecosystem R can be biometrically partitioned into leaf, stem and soil R by measuring samples of each component in chambers and upscaling the measurements to the stand level. The broad range of variation in the contribution of each component to R_{ECO} is partly due to stand structure, composition and age, but also to uncertainties in calculations. First, estimations of annual leaf respiratory C losses at the stand scale range from 3 to 37% of R_{ECO} in oak forests (Table 10.2). At an intra-annual scale, the largest contribution of leaf R to R_{ECO} generally occurs when new leaves expand; the lowest contribution can occur at peak summer drought in some evergreen Mediterranean forests (Rodríguez-Calcerrada et al. 2012). Second, the high proportion of parenchyma in the wood of oak species can make C losses from stems potentially important in oak-dominated ecosystems. The contribution of stem R to R_{ECO} in pure and mixed oak stands ranges between 5 and 38% on an annual basis, with mean values of ca. 15% (Table 10.2). The highest contribution of stem R to

R_{ECO} occurs in spring coincident with high stem growth rates in temperate and continental climates (Curtis et al. 2005; Miyama et al. 2006), and before water becomes limiting in the case of drought-prone Mediterranean regions (Rodríguez-Calcerrada et al. 2014). Third, soil R is the largest respiratory C flux to the atmosphere (Valentini et al. 2000) and accounts for 48–85% of R_{ECO} in oak forests (Table 10.2). Ambiguous discrimination between heterotrophic (microbes and soil fauna) and autotrophic sources of soil CO_2 efflux hinders accurate estimations of root R. Assuming an average contribution of soil R to R_{ECO} of 67% (Table 10.2), and a mean contribution of root R to soil R of 50% (Hanson et al. 2000; Burton et al. 2008), root R would account for 33% of R_{ECO}. More conservative contributions of root R to soil R observed in oak stands—ranging from 15 to 40% (Reichstein et al. 2002; Rey et al. 2002; Unger et al. 2009; Luan et al. 2011)—would reduce the contribution of root R to R_{ECO} to 10–27%, respectively. Furthermore, it is worth noting that neglecting internal fluxes of root respired CO_2 through xylem results in substantial underestimation of root R rates when these are estimated via soil CO_2 efflux measurements; underestimation ranges from 2 to 18% in *Quercus* species (Bloemen et al. 2014; Salomón et al. 2015) and reach up to 50% in other taxa (Aubrey and Teskey 2009). Overall, these estimates evidence the important role of autotrophic R in plant and ecosystem C budgets and further highlight the need of more experimental research on plant R to improve the accuracy of dynamic global vegetation models.

10.3   Volatile Organic Compounds (VOCs)

Plants produce a large array of metabolites whose vapor pressures are high enough (approx. $\geq$ 0.01 kPa) to become volatilized under ambient temperature conditions. All plant organs, namely flowers and fruits, foliage, stem and roots can release VOCs. Flower and leaf emissions are by far the best investigated ones. However, in the last decade increasing research has been afforded to root emissions, whose ecological roles in soil biotic interactions are only in the beginning to be appreciated (see e.g. Weissteiner et al. 2012; Delory et al. 2016). VOCs are emitted from plant organs either constitutively or temporarily following induction by stress factors. This classification is however not straightforward, because the emissions of constitutive VOCs are also up and down-regulated by environmental factors including stress events (Peñuelas and Staudt 2010).

Phytogenic VOCs are mainly composed of C and hydrogen plus occasionally other elements such as oxygen, nitrogen and sulphur, or more rarely halogens. Once emitted the C skeleton of VOCs reacts gradually with oxidants in the atmosphere to form ultimately CO_2, thus closing the carbon cycle. However, a substantial portion of intermediate products may be removed from the atmosphere via dry and wet deposition. Products from VOC oxidation can condense with each other and other atmospheric constituents and contribute to the formation of secondary organic

Table 10.2 Ecosystem respiration (R$_{ECO}$) in pure and mixed oak stands, and its partitioning (%) into leaf (R$_L$), stem (R$_S$[a]) and soil (R$_{SOIL}$) respiration

Stand	Site and climate	Stand characteristics	R$_{ECO}$ (g C m^{-2} year^{-1})	R$_L$	R$_S$	R$_{SOIL}$	Reference
Q. ilex coppice	Puéchabon (France) Mediterranean	5100 stems ha^{-1} 27.4 m^2 ha^{-1} 70 years-old	977	37	13	>50	Four studies[b]
Mixed oak[c]	Ozark (MO, USA) Continental	997 stems ha^{-1} >70 years-old	1684	10	15	>71	Li et al. (2012)
Mixed broadleaved[d]	Yamashiro (Japan) Temperate	5953 stems ha^{-1} 19.6 m^2 ha^{-1}	1080	21	16	63	Miyama et al. (2006)
Mixed harwood[e]	Michigan (USA) Continental	2214 stems ha^{-1} 29.7 m^2 ha^{-1}	1425	18	11	71	Curtis et al. (2005)
Temperate deciduous[e]	Massachusetts (USA)	20–24 m height 50–70 years-old	2460	28	5	68	Goulden et al. (1996)
Temperate mixed[f]	Changbai (China) Temperate	1556 stems ha^{-1} 43.2 m^2 ha^{-1} Uneven-aged	1490	31	21	48	Wang et al. (2010)
Mixed plantation[g]	Akou (Japan) Temperate	11,150 stems ha^{-1} 34 m^2 ha^{-1} 9 years-old	1144	36	Neglected	64	Kosugi et al. (2005)
Evergreen oak savanna[h]	Mitra (Portugal) Mediterranean	7.5 m height 21% tree canopy cover	568–1325	19–40	Neglected	60–81	Unger et al. (2009)
Deciduous-broadleaved[i]	Takayama (Japan) Cool-temperate	1379 stems ha^{-1} 50 years-old 20 m height	1397	24	10	67	Ito et al. (2007)
Q. robur forest steppe	Voronezh (Russia) Continental	Not reported	1205–1478	3–5	12–38	60–85	Molchanov (2009)

Data is presented on a yearly basis per unit of soil area. [a]R$_S$ estimated from CO$_2$ efflux measurements; R$_S$ commonly integrates branch respiration. [b]Data gathered from four studies in the same experimental site: R$_{ECO}$ from Rambal et al. (2014); R$_L$ from Rodriguez-Calcerrada et al. (2012); R$_S$ from Rodriguez-Calcerrada et al. (2014); R$_{SOIL}$ from Reichstein et al. (2002). [c]Q. alba, Q. velutina and Q. cocinea are dominant species; uniquely data from the unmanaged control plot is shown here. [d]Q. serrata is one of the dominant species. [e]Q. rubra is one of the dominant species. [f]Q. mongolica is one of the dominant species. [g]Q. serrata, Q. glauca and Q. phillyraeoides comprise ¼ of total basal area. [h]Q. ilex and Q. suber are dominant species. [i]Q. crispula is one of the dominant species

aerosols, which have important impacts on climate forcing and human health (Hallquist et al. 2009).

10.3.1   Metabolic Origins and Ecological Importance

Of the thousands existing plant VOCs, the majority belongs to three biosynthetic classes, fatty acid derived volatiles, volatile aromatic compounds and volatile terpenoids (isoprenoids). The most prominent fatty acid-derived VOCs are Green Leaf Volatiles (GLVs) that are formed from the breakdown of free fatty acids by lipoxygenase and hydroperoxide-lyase enzymes (Matsui 2006). GLVs comprise mainly mono-unsaturated C6 alcohols, aldehydes and acetate esters that are potentially emitted from all plant species. GLV are emitted in high amounts only after exposure to stresses such as wounding, herbivore attack, extreme temperatures or acute ozone exposure. Upon stress GLVs are formed and emitted within seconds to minutes and rapidly disappear when the stress ceases (e.g. Staudt et al. 2010). Volatile aromatic compounds derive from the shikimate pathway (benzenoids and phenylpropanoids). They are most common in flower scents (Schiestl 2010). However, recent studies made at plant and canopy levels emphasize that considerable amounts of benzenoids are also emitted from vegetative tissues in particular under stress conditions (Misztal et al. 2015). Volatile isoprenoids are classified according to the number of C5 units they have: C5 hemiterpenes, C10 monoterpenoids and C15 sesquiterpenoids. *In planta*, isoprenoids are synthesized within two distinct pathways, the 2-methyl-erythritol-4-phosphate pathway operating in plastids and the mevalonate pathway operating in the cytosol, endoplasmic reticulum and peroxisomes (Lu et al. 2016 and references therein). Volatile isoprenoids can also be secondarily formed from the breakdown of higher isoprenoids such as homoterpenes (Tholl et al. 2011) and apocarotenoids (Walter et al. 2010). The quantity and quality of emitted isoprenoids and aromatic compounds inherently differ among plant taxa. The hemiterpene isoprene is the most important VOC released from terrestrial vegetation. Globally ca. 600 Tg (10^{12} g) of isoprene are annually emitted, which is about 2/3 of the total biogenic VOC release (Sindelarova et al. 2014). However, only about 30% of vascular plants emit isoprene from their foliage (Fineschi et al. 2013). Oaks, poplars and willows figure among the strongest isoprene emitters (Kesselmeier and Staudt 1999).

In addition to the volatiles of these three major classes, a number of short-chain oxygenated volatiles (collectively called OVOCs) are frequently observed in plant emissions such as methanol, formaldehyde, formic acid, ethanol, acetaldehyde, acetic acid, methyl acetate, acetone, ethylene and methylglyoxal. These have different metabolic origins and occur rather universally in plants. For instance methanol is formed during cell wall formation and is therefore particularly released during the growing period (Bracho-Nunez et al. 2011; Brilli et al. 2016). With an estimated annual emission of ca. 130 Tg, methanol is the second important phytogenic VOC worldwide (Sindelarova et al. 2014). Emissions of ethanol and the

equivalent C2 aldehyde and acid are mostly associated with fermentation during hypoxia (Kreuzwieser and Rennenberg 2013). Many of these OVOCs are also secondarily formed during the oxidation of primary emitted higher VOCs such as terpenes (e.g. Gaona-Colmán et al. 2016).

Diverse ecological functions have been attributed to VOC production in plants. The attraction of pollinators and seed dispersers by flower and fruit scents is an essential driver of sexual reproduction and evolution in many plant species (Schiestl 2010). Further, numerous studies have shown that plant volatiles induced by herbivore or pathogen attacks have toxic, repellent or aposematic effects, or attract predators and parasitoids of the attackers and thereby contribute to limit damages to plants (see e.g. Van Loon et al. 2000). So far, such functions are largely unknown for oaks. Oaks are wind pollinated and a potential role of volatiles in sustaining acorn dispersal has rarely been documented (e.g. Verdú et al. 2007). Only few studies have reported that herbivory or pathogen attack affect quantitatively and/or qualitatively the volatile production from oaks (Staudt and Lhoutellier 2007; Paris et al. 2010; Copolovici et al. 2014). A study with *Q. robur* suggests potential beneficial effects of herbivory-induced VOCs against the European oak leaf roller (Ghirardo et al. 2012). On the other hand, Vuts et al. (2016) demonstrated that volatiles of *Q. robur* can attract the two-spotted oak buprestid, a bark beetle that causes severe damages in European oak forests.

The possible function of the constitutive isoprene production in chloroplasts (or analog monoterpenes) is still a matter of debate. With regard to biotic stress, a study using transgenic isoprene emitting *Arabidopsis* plants has shown that isoprene can disturb the attraction of a parasitic wasp to volatiles from herbivore-infested plants. Thus, by troubling VOC-mediated trophic interactions of neighbouring species, isoprene emitters could promote their interspecific competitiveness (Loivamäki et al. 2008). However, since isoprene is one of the most common background-VOC in the atmosphere, insects may rapidly adapt to avoid such interferences in host recognition (Müller et al. 2015). The major function of isoprene is thought to reinforce the resistance to abiotic stresses, in particular to oxidative and high temperature stress (see e.g. Loreto and Schnitzler 2010). The most pertinent results supporting these hypotheses were achieved with transgenic plants, either isoprene synthase over-expressing mutants of the non-isoprene emitting species *Arabidopsis* (Sasaki et al. 2007; Velikova et al. 2012) and tobacco (Vickers et al. 2009b; Tattini et al. 2014) or isoprene synthase silenced mutants of the isoprene emitting species poplar (Behnke et al. 2007, 2010). However, several studies using the same or other transgenic mutants reported conflicting results with respect to these hypotheses (Behnke et al. 2009, 2012; Palmer-Young et al. 2015). Further, it is uncertain that the improved resistance to abiotic stress in isoprene emitters is, as initially hypothesized, due to direct effect of isoprene by scavenging oxidants or stabilizing membrane structure. In fact, isoprene dissolves too little in bio-membranes to efficiently change membrane conformation (Harvey et al. 2015) and is only fairly suitable to scavenge oxidants due to its moderate reactivity (Atkinson and Arey 2003; Palmer-Young et al. 2015) and the high toxicity of reaction products (Cappellin et al. 2017; Matsui 2016 and references therein). More likely, the

physiological effects of isoprene are indirect by taking part in the plant's stress signalling network (Vickers et al. 2009a; Vanzo et al. 2016). In any case, the genetically engineered absence or presence of isoprene synthase in mutants causes transcriptomic, proteomic and metabolic changes in various metabolic pathways even under non-stress conditions, including the biosynthesis of phenyl-propanoids and lipids that affects the composition and ultrastructure of chloroplast membranes (Velikova et al. 2015; Harvey and Sharkey 2016). Numerous other VOCs than isoprene have shown to be involved in within-plant and between-plant stress signalling, among which diverse GLVs, aromatic compounds and higher isoprenoids (Havaux 2014; Delory et al. 2016; Matsui 2016).

10.3.2   Diversity of VOCs in Oak Species

The great majority of oak species hitherto screened for VOC emission has been found to release isoprene constitutively at high rates from its foliage (up to several tenths of nmol $m^{-2} s^{-1}$). However, several oak species with distribution around the Mediterranean do not produce isoprene, but produce either monoterpenes in high amounts or shown no constitutive VOC emissions. These exceptions are mostly but not exclusively evergreen oaks and belong all to the two very closely groups *Cerris* and *Ilex* (Welter et al. 2012; Monson et al. 2013). Diversification of isoprene emission in oaks has been mainly observed at species and higher taxon levels and more rarely at population level. So far, inherent intra and/or inter population variability in the quantity or quality of constitutively produced VOC has not been reported within isoprene emitting oak species (Welter et al. 2012; Steinbrecher et al. 2013). By contrast in monoterpene emitting species, compositional diversification (i.e. chemotypes) has been frequently observed within and among populations (Staudt et al. 2001b, 2004; Loreto et al. 2009; Welter et al. 2012). In addition, a few low or non-emitting individuals were detected in some monoterpene emitting populations. Conversely, dual isoprene/monoterpene emitting oak individuals seem to be extremely rare in natural oak populations (Staudt et al. 2004). This is somewhat surprising, because many oaks can hybridize with each other resulting in widespread genetic introgression or rise of new species (e.g. Valbuena-Carabaña et al. 2007). For example, the endemic oak *Q. afares* (Algerian oak) is considered to be a stabilized hybrid between *Q. suber* and *Q. canariensis*. Yet, *Q. afares* produces exclusively monoterpenes (Welter et al. 2012) as one of its parent species (*Q. suber*), but seems to have completely lost or suppressed the VOC production capacity of its second parent *Q. canariensis*, which produces only isoprene. These findings indicate that qualitative diversification in the monoterpene production capacity occurs frequently and has no or only minor consequences for the competitiveness of the trees. By contrast, the loss or gain of isoprene synthesis happens more rarely during species evolution, possibly because it requires co-evolving compensatory mutations to overcome failures in metabolic homeostasis.

10.3.3   Response to Environmental Changes at Different Time Scales

Unlike for CO_2 and water vapor, the foliar exchange of VOCs is less constrained by stomatal conductance. This is due to their generally low gas phase concentrations inside the leaves, which allow changes in the diffusive resistance by stomata movements to be compensated by concomitant changes in the concentration gradients between the substomatal cavity and the outer atmosphere. Nevertheless, many OVOCs are at least partly under stomatal control either because these VOCs are transported with the transpiration stream and/or because these VOCs dissolve efficiently in liquid phase, which in turn delays the re-equilibrium of the gaseous concentration in the apoplast in response to stomata movements (Niinemets et al. 2002). In any case, all VOC emissions are strongly modulated by external factors, above all temperature, which governs the VOC's vapor pressures and diffusion velocities, in addition to metabolic processes involved in the VOC release (Staudt et al. 2017b). In oaks, the major bulk of the emitted VOCs (constitutive isoprene and monoterpenes) is directly regulated by their synthesis rate inside the chloroplasts, which in turn depends on the availability of primary substrates coming from light-dependent photosynthetic processes. Recent studies on poplar suggest that most of the short-term variation of isoprene emission is due to limitations in the availability of reduction power from photosynthetic electron transport (Rasulov et al. 2016 and references therein). Thus, constitutive isoprene and monoterpene emissions from oaks, and perhaps also stress-induced de novo synthesized emissions of sesquiterpenes, are strongly and almost instantaneously modulated by both temperature and light (e.g. Staudt and Lhoutellier 2011). The shape of the emission response to light resembles that of net photosynthesis; i.e. a rectangular hyperbola approaching an asymptote at high light values (Staudt and Bertin 1998). By contrast, the temperature response exhibits a shape typical for the temperature dependence of enzyme-catalyzed reactions (Fig. 10.2). In addition to these fast responses, light and temperature modulates the oak's overall emission capacity over the seasons with changing weather conditions (e.g. Pier and McDuffie 1997; Staudt et al. 2002, 2003, 2017a) mostly via the expression of genes of rate-limiting enzymes (Schnitzler et al. 1997; Fischbach et al. 2002; Lavoir et al. 2009). Constitutive isoprenoid emissions from oaks are also influenced by other environmental factors such as ozone (Velikova et al. 2005), atmospheric CO_2 concentration (Loreto and Sharkey 1990; Staudt et al. 2001a) or shortage and excess of soil water (Bertin and Staudt 1996; Staudt et al. 2002, 2008; Rodríguez-Calcerrada et al. 2013; Bourtsoukidis et al. 2014; Saunier et al. 2017).

10.3.4   Relative Importance for Tree Carbon Budgets

Given that in oaks almost all primary C substrate used in the biosynthesis of volatile isoprenoids comes from ongoing photosynthesis, the C loss associated with

emission can be expressed as the ratio of mol emitted C to mol assimilated C. As shown in Fig. 10.2, the instantaneous C loss varies much with changing temperature but little with light. Under most conditions the instantaneous C loss of
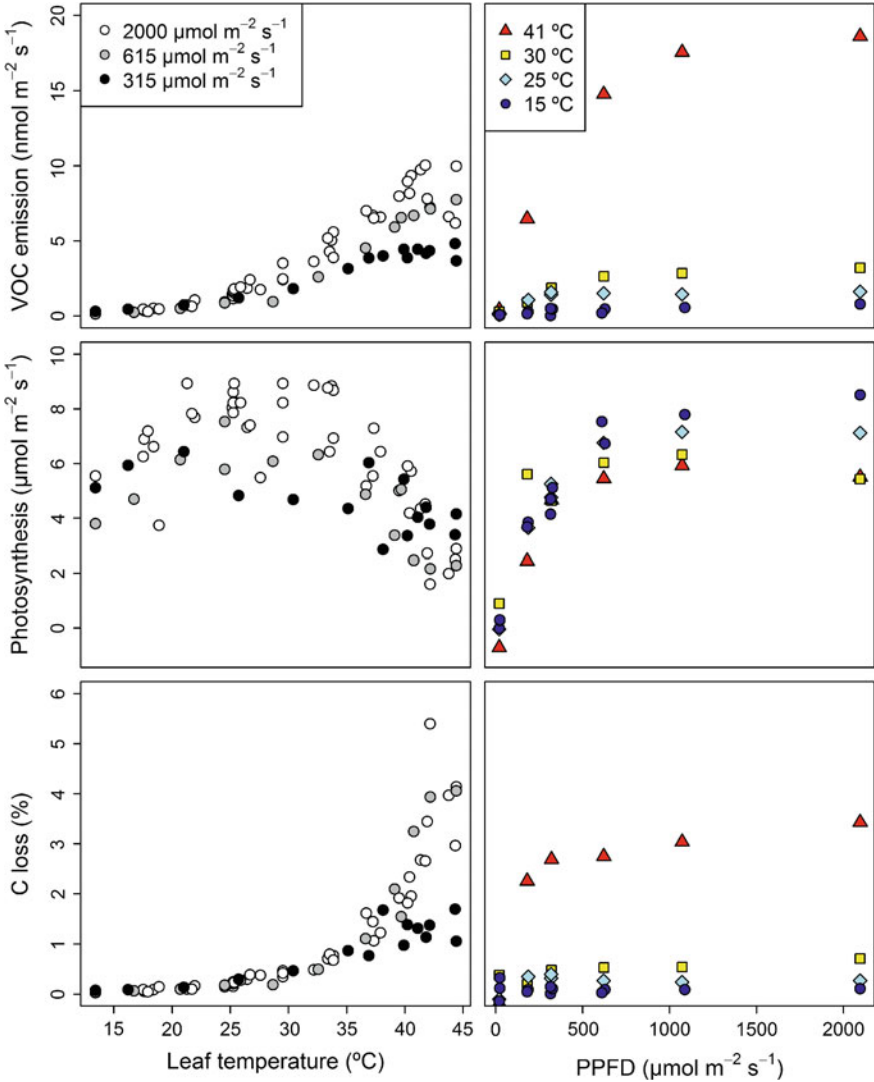

Fig. 10.2 Effects of temperature (left) and light intensity (photosynthetic photon flux density (PPFD), right) on monoterpene emission (upper graphs), photosynthesis (middle graphs) and the resulting relative carbon loss from monoterpene emission (C loss, lower graphs) in *Q. ilex* leaves. Temperature effect was measured at a PPFD of about 315, 615 and 2000 μmol m^{-2} s^{-1}. Light effect was measured at a temperature of about 15, 25, 30 and 41 °C. Data were compiled from Staudt and Bertin (1998)

assimilated C by constitutive isoprenoid emissions will be less than 1%. However, during heat spells, the C loss can substantially increase, especially when combined with drought events. In fact, isoprenoid emissions from oaks are less sensitive to water shortage than photosynthesis. The emissions decrease only when drought is severe while under mild drought they remain stable or even increase (Fig. 10.3). As a result, VOC emissions from oaks may significantly drain photosynthetic C and energy during conditions in which other sinks associated with growth are inhibited. In addition to constitutively produced isoprenoids, new volatiles induced by abiotic or biotic stresses may further exhaust the tree's C resources. The exact C loss by these emissions is difficult to assess since stress usually induces a wealth of high-molecular, very reactive trace compounds (many of which remain undetected) that are emitted sporadically. Generally, the emission rates reported for stress-induced VOCs are lower than those for strong constitutive isoprenoid emissions. For instance, in *Q. ilex* leaves VOC emissions induced by gypsy moth infestation (mainly sesquiterpenes and homoterpenes) accounted for about 10% of the total foliar VOC release (Staudt and Lhoutellier 2007).

The emissions of OVOCs from foliage have often been neglected when estimating C losses by VOC emission, because their accurate measurement requires different techniques to that of common VOCs. However, as mentioned above, many of them are ubiquitous plant volatiles that can be emitted at quite high rates, such as methanol. By combining PTR-MS technique with classical GC-MS, Bracho-Nunez et al. (2013) determined a large range of VOC exchange in 28 plant species, among which three oak species. At standard light and temperature conditions, mean C loss of net-photosynthesis by VOC emission ranged between 1.4 and 3.7%, with methanol and acetone contributing between 5 and 66% to the total VOC release. The quantities of VOCs released from roots and stem tissues are only poorly known and to our knowledge have never been reported for oaks. Nevertheless, Weissteiner et al. (2012) identified more than 60 VOCs in the headspace of washed healthy and damaged roots of young *Q. petraea* × *Q. robur* trees, of which 13 compounds were consistently released. Asensio et al. (2007) investigated the VOC exchange of soil in a *Q. ilex* forest and concluded that it represented 0.003% of the total C emitted by soil as CO_2.

On the other hand, there is increasing awareness that VOC exchanges can be bidirectional at least for some OVOCs and hence compensation points in VOC concentration exist, above which VOCs are taken up by plants (Niinemets et al. 2014; Matsui 2016 and references therein). For example, Staudt et al. (2000) observed bidirectional exchanges of acetic acid from diverse plant species, with net emissions dominating during day-time and net depositions dominating during night-time. For *Q. ilex*, the average deposition rate observed in darkness was more than half of the average emission rate observed under illumination (0.41 and 0.72 ng C m^{-2} s^{-1}, respectively). Furthermore, secondary VOCs produced during atmospheric oxidation can be taken up by the vegetation and metabolized, thus possibly recovering parts of the C lost by emission (Karl et al. 2010; Park et al. 2013). Bidirectional above-canopy VOC fluxes have been recently measured by Schallhart et al. (2016) in a mixed oak forest during the early summer season. These
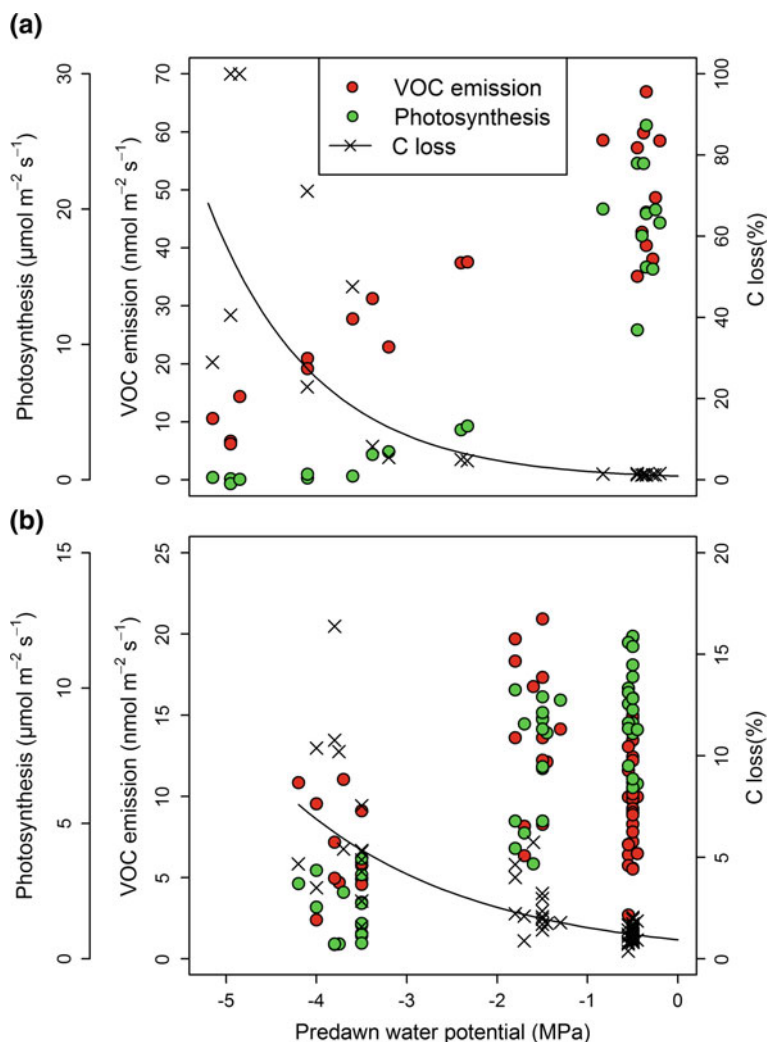
Fig. 10.3 Plot of isoprenoid emissions, photosynthesis and resulting relative C losses from isoprenoid emissions against predawn water potential during two drought experiments on *Quercus pubescens* (**a**, isoprene emitter) and *Quercus suber* (**b**, monoterpene emitter). Oak saplings were exposed to one or two consecutive drying cycles for *Q. pubescens* and *Q. suber*, respectively. Gas exchange measurements were made under the same standard light and temperature conditions (1000 µmol m^{-2} s^{-1} PPFD; 30 °C). Lines are best fits on C-loss data assuming an exponential relationship for *Q. pubescens* (R^2 = 0.92; Rodríguez-Calcerrada et al. 2013) and *Q. suber* (R^2 = 0.67; Staudt et al. 2008)

authors observed an average net VOC efflux to the atmosphere of 41.8 nmol C m^{-2} s^{-1} which accounted for a bit less than 2% of the net uptake of CO_2. This number likely represented the upper limit of VOC-related C loss in that study site, because

the measurements were conducted during the season when the emission capacity for constitutive isoprenoids reaches usually its maximum. Continuous online year-long measurements of total VOC exchanges at plant or canopy levels are still sparse due to methodological constraints. As an exception, Brilli et al. (2016) have monitored by eddy covariance both VOC and CO_2 exchanges over a temperate poplar plantation throughout a whole growing season. Although poplar is, similar to most temperate oak species, a strong isoprene emitter, they observed a relatively small net VOC flux of ca. 1 g m^{-2} per growing season accounting for about 0.8% of the net ecosystem CO_2 exchange. Earlier studies extrapolated discontinuous VOC emission/flux measurements by means of generic emission models to assess their weight relative to annual ecosystem C budget. For example Kesselmeier et al. (2002) estimated the annual C loss by VOC emission from an evergreen oak Mediterranean forest being 0.45% of their annual GPP.

10.4   Rhizodeposition

The rhizosphere is a highly populated environment. There are thousands of non-volatile organic compounds released by roots that mainly consist of carbohydrates, amino acids, vitamins, lipids, and a wide variety of secondary metabolites and proteins. Rhizodeposits can alter the physico-chemical soil properties and play important roles in the interactions of the plant with microbes or competing plant species (Bais et al. 2004; Bashir et al. 2016). As example, phenolic compounds help roots to deter the attack of pathogens (Lanoue et al. 2010); flavonoids facilitate the mutualistic symbiosis with mycorrhizal fungi (Nagahashi et al. 2010); the synthesis and release of some enzymes increase the availability of phosphorus forms that are absorbable by the roots (Dakora and Phillips 2002); while the exudation of phospholipids by root tips can reduce the surface tension of the soil solution and enhance the uptake of water and nutrients (Read et al. 2003). Similar interactions might exist in the rhizosphere of oak trees. However, the function and chemical profiling of rhizodeposits have been rarely studied within this genus. One of the scarce studies documents the effect of herbivory on C rhizodeposition in 2-year-old *Q. rubra* seedlings (Frost and Hunter 2008): It was observed that foliar herbivory reduced C allocation to fine roots whilst root exudation was actively regulated to maintain constant rates of C rhizodeposition, likely to sustain nutrient supply to microbes.

Rhizodeposition is affected by edaphic and environmental factors (reviewed by Nguyen 2009). The abundance of soil microorganisms substantially enhances the allocation of C assimilates to the rhizosphere. Besides, soil texture affects microbial activity, nutrient cycling, and soil physical properties, so that rhizodeposition increases in loam and clay soils due to their higher fertility and the smaller size of soil pores that facilitate the flow of organic compounds. Regarding climatic conditions, rhizodeposition is expected to increase during drought stress (Henry et al.
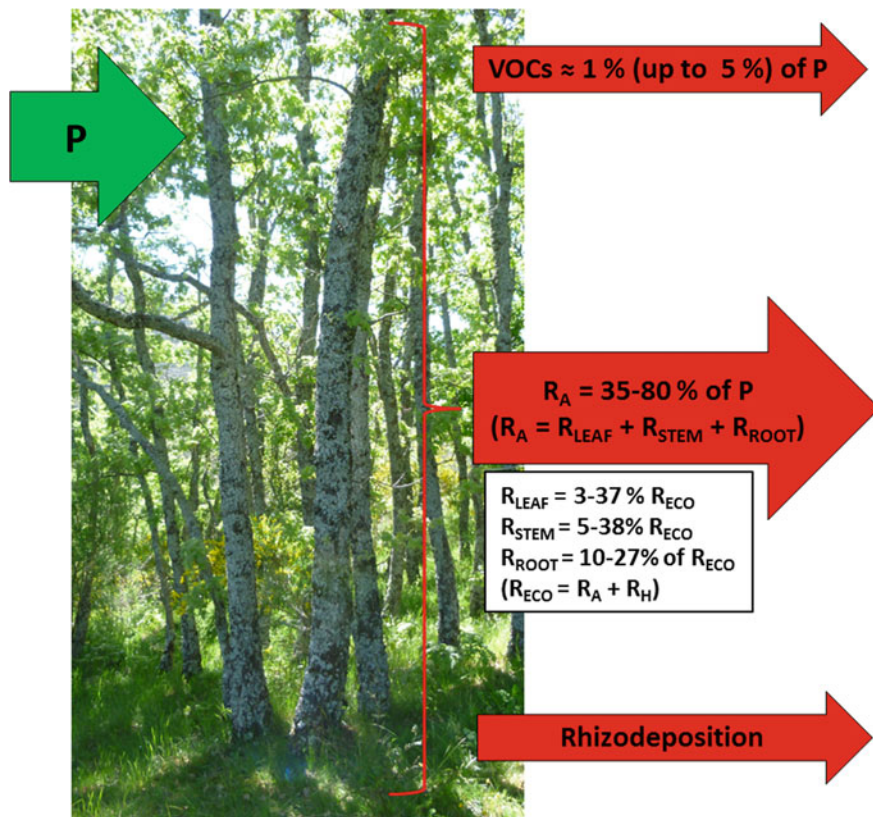
Fig. 10.4 Simplified schematic of tree carbon (C) budget in an oak forest. Net primary production can be estimated as the difference between photosynthesis (P) and overall C loss. Tree C loss occurs via emission of volatile organic compounds (VOCs), autotrophic respiration (R_A), and rhizodeposition of organic compounds. Autotrophic respiration is partitioned into leaf, stem and root respiration (R_{LEAF}, R_{STEM} and R_{ROOT}, respectively) and is expressed as a fraction of ecosystem respiration (R_{ECO}), which additionally integrates heterotrophic respiration (R_H) of living organisms in the soil

2007), and seems to be unaffected by changes in atmospheric [CO_2] (Nguyen 2009).

For experimental simplicity, research on rhizodeposition has focussed on herbaceous plants and young tree seedlings (<2 months old; reviewed by Jones et al. 2009), so that any extrapolation to large trees would be biased by the potential effect of plant age on C allocation patterns (Nguyen 2009). Assessments on the contribution of C rhizodeposits to plant C budgets is an experimentally elusive task, mainly because of the technical limitation that the soil imposes for the quantification of C flow through the rhizosphere, and the natural abundance of soil microorganisms that promptly assimilate rhizodeposits. We are aware of only one study in which the contribution of C rhizodeposits to tree C budgets has been

surveyed in oak species. In mature trees of *Q. serrata* and *Q. glauca*, C loss via root exudation was proportional to that of root R (10%) on a root-weight basis, and accounted for 3% of NPP (Sun et al. 2017). Similarly, studies on annual herbs and tree seedlings using isotopic tracers estimate that the portion of C assimilated through photosynthesis and lost via rhizodeposition ranges between 2 and 11% (Jones et al. 2009; Preece and Peñuelas 2016). However, these rough estimates should be taken with caution due to the uncertain origin and fate of C within the rhizosphere (Jones et al. 2009). Finally, there is increasing evidence that roots of autotrophic plants can take up amino-acids hence assimilating organic C and nutrients (reviewed by Schmidt et al. 2013). This mixotrophic behaviour has been observed in *Q. petraea* roots during spring, when the strong C demand for growth before budburst cannot completely rely in new assimilates (Bréda et al. 2013), thus adding further complexity to the estimation of net C loss belowground.

10.5   Conclusions

Carbon assimilation traditionally occupies a predominant role in the study of tree C cycling, whereas processes involved in the C release from the plant to the atmosphere are comparatively understudied. Respiration, emission of VOCs and rhizodeposition constitute therefore the overlooked side of tree C budgets, included those of oak trees. The ecological importance, physiology and environmental control of R and VOC emissions in oak species have been reviewed; a simplified schematic of the tree C budget in oak—dominated stands is presented in Fig. 10.4. Autotrophic R is expected to consume half of the assimilated C, with respiration—to—photosynthesis ratios ranging between 35 and 80%. The relative contribution of leaves, stems and roots to the overall C respiratory expenditure largely fluctuates according to stand structure, composition and age (Table 10.2). The C loss associated with VOC emissions accounts for about 1% of gross P. This percentage may increase up to 5% during heat waves and under drought stress (Figs. 10.2 and 10.3), and even more if VOCs emitted from flowers, fruits, stems and roots are taken into account. Rhizodeposits represent an additional and non-negligible source of tree C loss. However, scarce literature on oak rhizodeposition discourages attempts to provide a rough quantitative estimation. Furthermore, environmental—induced fluctuations in oak R and VOC emissions are not necessarily proportional to fluctuations in C assimilation. Thus, the assumption of homeostatic ratios between C loss and C gain should be revisited as it might lead to erroneous predictions on the strength of oak stands as C sinks in a climate changing world, conclusion that could be extrapolated to other tree taxa. A comprehensive understanding of oak C loss comparable to that of photosynthesis would be therefore necessary to accurately assess oak C cycling in scenarios of climate change.

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