REVIEW PAPER

Walnut (*Juglans* spp.) ecophysiology in response to environmental stresses and potential acclimation to climate change

Martin-Michel Gauthier · Douglass F. Jacobs

Abstract

• **Context** Walnuts (*Juglans* spp.) are ecologically and commercially important trees, yet synthesis of past and current research findings on walnut ecophysiology is lacking, especially in terms of potential acclimation to climate change.

• **Aims** This study aims to (1) investigate walnut ecophysiology by comparing its attributes to associated deciduous angiosperms, (2) address potential acclimation of walnut to climate change, and (3) identify areas for prioritization in future research.

• **Results** There is considerable uncertainty regarding the magnitude of potential effects of climate change on walnut. Some studies tend to indicate walnut could be negatively impacted by climate change, while others do not. Walnut may be at a disadvantage due to its susceptibility to drought and frost injury in current growing regions given the projected increases in temperature and extreme climatic events. Other regions that are currently considered cold for walnut growth may see increased establishment and growth depending upon the rate of temperature increase and the frequency and severity of extreme climatic events.

• **Conclusion** Research investigating a combination of environmental factors, such as temperature, carbon dioxide, ozone, water, and nitrogen is needed to (1) better project climate change effects on walnut and (2) develop management strategies for walnut acclimation and adaptation to climate change.

Keywords Climate change · Ecophysiology · Environmental stress · *Juglans* · Walnut

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1 Introduction

The walnut genus (*Juglans* spp.) contains some of the most economically and ecologically valuable trees species in America, Europe, and Asia. Of the 20 species found worldwide, black walnut (*Juglans nigra* L.) and English walnut (*Juglans regia* L.) are the most abundant species of the genus and most commonly represented in the literature. Black walnut is dispersed throughout the central and eastern USA and is highly prized for its lumber. English walnut is also found scattered throughout Europe and Asia and is valued both for nut and lumber production (Hardin et al. 2001). In the western USA, English walnut and its associated hybrids are cultivated for nut production with an estimated crop value of US $700 million (USDA 2009). Nuts are also an important food source for wildlife, such as squirrels (*Sciurus* spp.) (Smith and Follmer 1972). In recent years, a growing number of reports were published on physiological responses of walnut species to environmental factors, such as water, temperature, and nutrients. Many of these studies were conducted to address climate change issues, such as understanding decreased growth or survival due to the reduction in accumulated winter chill and increased freeze–thaw events for nut production in France

(Améglio et al. 2004), the western USA (Baldocchi and Wong 2008; Luedeling et al. 2009a), and Southwest Asia (Luedeling et al. 2009b). Even studies not specifically aimed at investigating climate change can be useful in identifying physiological attributes of species that may become critical in relation to projected changes in climate, i.e., response to increased temperature or decreased precipitation. To our knowledge, there are no published reports that synthesize this body of work. Thus, the objectives of this review were to (1) investigate walnut ecophysiology and compare features to associated deciduous angiosperms, (2) address potential acclimation of walnut to climate change, and (3) identify areas for prioritization in future research. Insufficient scientific literature on the ecophysiology of other walnut species, such as butternut (*Juglans cinerea* L.), did not allow their inclusion in this review.

The literature reviewed on walnut stress physiology includes more than 100 articles that cover most of the research carried out in the last 35–60 years. The literature was grouped into four categories based on major plant functions: (1) carbon dynamics and photosynthesis, (2) nutrient functions, (3) acclimation to temperature, and (4) water relations. About half of all experiments studied English walnut or one of its associated hybrids; the other half investigated black walnut. Comparisons where often made with associated species, such as oak (*Quercus* spp.) and maple (*Acer* spp.), to contrast responses of species with different ecological and physiological attributes.

2 Carbon dynamics and photosynthesis

2.1 Carbon dynamics

Most of the literature on walnut C dynamics was carried out during the first or second year of development. Like oaks and other large-seeded species, walnut uses carbohydrates stored in the maternal seed to develop its taproot (Maillard et al. 1994a). For the first 3 weeks after sowing, the seedling is entirely heterotrophic, i.e., its growth depends exclusively on the seed's C reserves (Maillard et al. 1994a; Fig. 1a). Photosynthesis begins thereafter but is negligible until the second month of growth (Maillard et al. 1994a). In plantlets provided with a growing medium, autotrophy can be attained 8 days after transfer to a growth chamber (Chenevard et al. 1997), but seedlings need at least 40–50 days before they no longer depend on the maternal seed (Maillard et al. 1994a, b). Leaves are both a sink and a source of C during the second month, accounting for nearly 60% of all C in the plant (Fig. 1b). From days 32 to 48 after sowing, photosynthesis increases and leaves can allocate about 15% of labeled C to the stem. For the remainder of the second month, C produced by leaves is mostly allocated
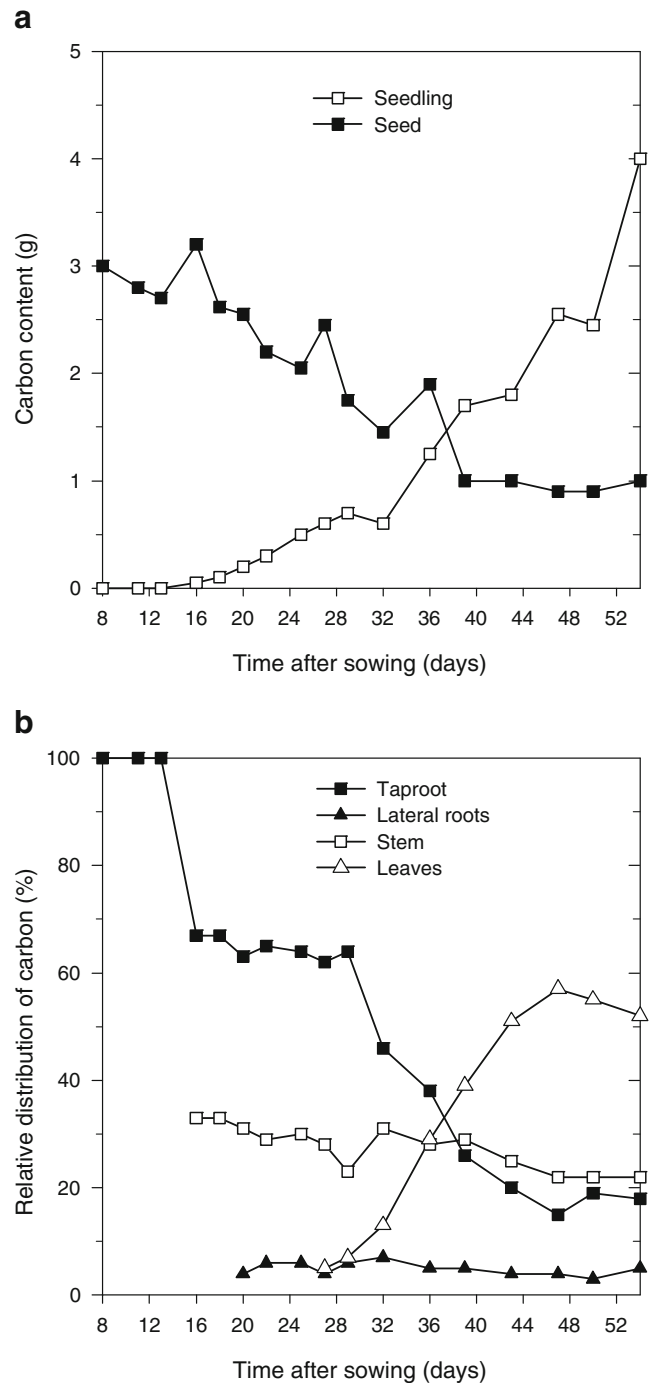
Fig. 1 Variation of carbon in an English walnut seedling (*J. regia* L.) and its maternal seed (**a**) and relative distribution of carbon in various organs of an English walnut seedling (**b**) under controlled conditions (22°C, 12 h) during the first 2 months of development. Each value is the mean obtained from the combustion of dry matter of a set of five plant samples (Maillard et al. 1994b, by permission of Oxford University Press)

to the taproot and lateral roots (Maillard et al. 1994b). During the first growing season, most of the C fixed through photosynthesis is accumulated in the taproot (~90%) as starch, a large portion of which will serve as a

source of carbohydrates for subsequent development (Lacointe 1989; Lacointe et al. 1993; Chenevard et al. 1994; Maillard et al. 1994a, b).

Published literature on walnut C dynamics in saplings or trees is less abundant, but research findings indicate remobilization can be substantial in this genus (Table 1). In this regard, walnut is similar to most tree species that accumulate large pools of non-structural carbohydrates (NSC), such as starch (Millard and Grelet 2010). In deciduous angiosperms, NSC levels are never fully depleted and are often at a maximum in late summer and early autumn (Millard and Grelet 2010). In 3-year-old English walnut, C accumulated as starch in the taproot in late summer and fall can be hydrolyzed to sugar in winter and remobilized by growing organs in spring (Frossard and Lacointe 1988; Lacointe et al. 1993). Lacointe et al. (1995) also reported that recent (up to 5 days old) C fluxes allocated toward respiration did not exceed 25% of total plant respiration as measured in August and October using $^{14}CO_2$ labeling in young English walnut trees. While changes in temperature and demand from sink organs are thought to be important causal mechanisms in walnut C remobilization, the relative importance of each mechanism is still uncertain (Lacointe 2000). A recent review by Millard and Grelet (2010) tends to suggest C remobilization in tree species is largely sink-driven.

Walnut's period of active photosynthesis and therefore potential annual C gain is restricted relative to associated species by its shorter period of full leaf out and determinate shoot growth habit. Walnut exhibits comparatively later (~2 weeks) spring bud break (Lechowicz 1984) and earlier (~1 month) leaf fall senescence (Lucier and Hinckley 1982). As a result, walnut seedling growth is relatively rapid. In 1-year-old, field-grown black walnut, Carpenter and Hanover (1974) found that 73% of height growth occurred 1 month after bud break and 100% of stem growth and leaf area accretion occurred 2 months after bud break. Honeylocust (Gleditsia triacanthos L.), a shade-intolerant, associated species with an indeterminate growth habit displayed much slower growth compared to walnut: 60% of height growth, 50% of stem growth, and 68% of leaf area accretion occurred during the same time period. When the period of active photosynthesis is not taken into account, black walnut height growth is generally slower than yellow-poplar (Liriodendron tulipifera L.) or white ash (Fraxinus americana L.) but higher than oak species on good sites (Williams 1990). Some studies reported English walnut root and shoot growth occurred simultaneously during the first year (Frossard et al. 1989), while others did not (Maillard et al. 1994b). This periodicity can also change over time, as root development was found to occur after leaf and shoot growth during the second year (Frossard et al. 1989).

Table 1 Selected ecological and ecophysiological attributes of walnut (*Juglans* spp.) relative to associated deciduous angiosperms

Ecological features	Relative level	Uncertainty	Selected references
Shade tolerance	Low	Low	Baker 1948; Williams 1990
Growth rate	Average	Low	Carpenter and Hanover 1974; Williams 1990
Susceptibility to frost injury	High	Low	Fady et al. 2003; Poirier et al. 2010
Susceptibility to embolism	High	Low	Améglio et al. 2002; Bréda et al. 2006
Desiccation avoidance (susceptibility to drought)	High	Low	Davies and Kozlowski 1977; Hinckley et al. 1979
Flood avoidance (susceptibility to flooding)	High	High	Mapelli et al. 1997; Dudek et al. 1998
Rooting depth	High	Low	Pallardy and Rhoads 1993; Williams 1990
Nutrient requirements	High	Low	Thompson and McComb 1962; Schlesinger and Funk 1977
Ecophysiological features	Relative level	Uncertainty	Selected references
C and N accumulation and remobilization	Average	Low	Lacointe 1989; Maillard et al. 1994a, b; Millard and Grelet 2010
Period of active photosynthesis and potential C gain	Low	Low	Lechowicz 1984; Lucier and Hinckley 1982
Capacity for photosynthesis (A, A_{max}) and respiration (R_d)	High	Low	Piel et al. 2002; Gauthier and Jacobs 2010
Capacity for light acclimation	Average	Low	Dean et al. 1982; Frak et al. 2001
Capacity to sustain repeated freeze–thaw events	Low	Low	Améglio et al. 2001c, 2002
Temperature inducing photoinhibition	Average	High	Dreyer et al. 2001
Stomatal sensitivity to humidity	High	Low	Ni and Pallardy 1990, 1992
Capacity for leaf abscission	High	Low	Ni and Pallardy 1991; Tyree et al. 1993
Response to elevated CO_2	High	High	Tinus 1976; Maillard et al. 1999
Response to elevated O_3	Unknown	High	None

Uncertainty is based on the number of studies conducted on the subject and the level of agreement among them

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## 2.2 Photosynthetic capacity and acclimation

Walnut has long been considered intolerant of shade (Baker 1948; Williams 1990; Hardin et al. 2001). Shade-intolerant species generally exhibit thicker leaves with lower quantum efficiency (Q_e, micromoles of CO_2 per micromole photons) and higher light-saturated maximum photosynthesis (A_{max}, micromoles of CO_2 per square meter per second) compared to leaves of shade-tolerant species (Loach 1967; Kozlowski and Pallardy 1997). Black walnut can also carry out substantial rates of net photosynthesis (A, micromoles of CO_2 per square meter per second) during the growing season past the sapling stage (Gauthier and Jacobs 2010). These acclimations reflect the fact that shade-intolerant species require high light conditions to develop, where investments in increased mesophyll thickness allow greater photosynthate production. Findings from Dean et al. (1982) indicate that black walnut can carry out considerable A under shaded conditions for short periods of time at the juvenile stage. In contrast to walnut, shade-tolerant species such as sugar maple (*Acer saccharum* Marsh.) develop thinner leaves that capture light more efficiently (higher Q_e) and initiate A at lower light levels (~0–200 µmol photons m^{-2} s^{-1}).

Like all plants (Niinemets 2007), walnut exhibits photosynthetic plasticity to light. Walnut's photosynthetic acclimation and distribution of leaf characteristics, such as leaf mass per unit area (LMA) and leaf N content per unit area (N_a), are influenced by light level, light quality (red/far red ratio), and light source (Le Roux et al. 1999a; Green and Kruger 2001; Frak et al. 2002a, 2005; Rosati et al. 2004). Walnut's crown architecture varies according to the light environment to maximize C gain (Le Roux et al. 1999b, 2001; Sinoquet et al. 2001). For example, sun leaves of English walnut were found to have greater A_{max}, stomatal conductance (g), LMA, N_a, and lower dark respiration (R_d, micromoles of CO_2 per square meter per second) compared to shade leaves of the same species (Piel et al. 2002). Within the crown of a 20-year-old English walnut tree, LMA was shown to vary from 50 to 150 gm^{-2} and N_a varied from 1 to 3 gm^{-2} along a south–north horizontal transect (Le Roux et al. 1999b). The highest values were located on the southern edge and at the top of the canopy. A similar study also found spatial variation in leaf ^{13}C isotope composition (~25–30‰) in the crown of an isolated English walnut tree (Le Roux et al. 2001).

The amount of time required for walnut to acclimate to changing light conditions increases with leaf age (Frak et al. 2001) and plant development stage (Gauthier and Jacobs 2009). Transferring 1-year-old English walnut hybrids from low light (10% incident radiation) to high light (90% incident radiation) environments increased photosynthetic capacity by 25–45% within 20 days (Frak et al. 2001). Seedlings exhibited weak photosynthetic

acclimation when transferred 91 days after bud burst in 1 year but were able to acclimate when transferred 58 days after bud burst in the next year (Frak et al. 2001). Acclimations were mainly due to changes in leaf N_a and leaf N partitioning among photosynthetic functions, such as carboxylation, bioenergetics, and light capture. Similar experiments conducted with northern red oak (*Quercus rubra* L.) and sugar maple at the seedling stage showed that time required for photosynthetic acclimation was comparable to results from Frak et al. (2001), despite species differences in shade tolerance (Naidu and DeLucia 1997). These findings also highlight the importance of N in walnut's photosynthetic acclimation to light. Acclimation to increased light may take longer (1 year) in black walnut trees past the sapling stage (Gauthier and Jacobs 2009).

Walnut's photosynthetic capacity and acclimation response to elevated CO_2 and O_3 is still poorly documented (Tinus 1976; Maillard et al. 1999). A five-fold increase in CO_2, from 325 to 1500 µmol mol^{-1}, generated growth increases of 70% in dry mass of black walnut seedlings (Tinus 1976); the length of the measurement period and the age of the seedlings were not specified. Maillard et al. (1999) grew English walnuts from seed for 55 days under controlled chamber conditions to investigate C and N allocation patterns under two CO_2 levels. Although not statistically confirmed, the 45% increase in CO_2, from 550 to 800 µL L^{-1}, doubled the C content of seedlings by the end of the measurement period (Fig. 2). Elevated CO_2 also impacted C allocation by increasing the root/shoot ratio. In a synthesis of the literature, Wullschleger et al. (1995) compared relative growth responses of 73 tree species to a doubling of ambient CO_2. Among
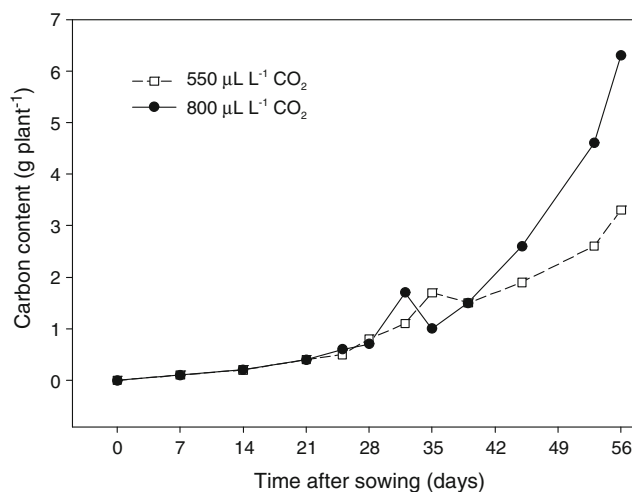
Fig. 2 Influence of elevated CO_2, from 550 to 800 µL L^{-1} (46% increase), on the total carbon content of germinating English walnut (*J. regia* L.) seedlings. The end of seed C contribution occurred on day 35. Mean value was calculated from three replicates originating from a sample of five to ten seedlings. Source: Maillard et al. (1999), http://www.afs-journal.org/

all species studied, black walnut ranked 15th in terms of relative increase in total plant dry mass (46%) based on findings from Tinus (1976). Among temperate hardwoods, black walnut ranked third behind sugar maple (11th) and American beech (*Fagus grandifolia* Ehrh., 14th) but higher than northern red oak (25th) and white oak (*Quercus alba* L., 53rd). We did not find any literature investigating effects of elevated O_3 in this genus.

In comparison to these studies, short-term (7 years) results from one of the free-air CO_2 enrichment (FACE) experiments showed that 46–54% increases in atmospheric CO_2 increased net primary productivity (NPP) of northern temperate hardwood forests of the USA by 25% to 60% compared to nontreated controls (King et al. 2005). Across four sites distributed in the USA and Europe, median gains in NPP from elevated CO_2 (550 μmol mol^{-1}) were calculated at 23% based on 10-year data from FACE experiments (Norby et al. 2005). More recent results showed declining N availability reduced these gains, thus stressing the importance of N on C gain and productivity at the forest scale (Norby et al. 2010). Results from King et al. (2005) also indicate that 34–45% increases in elevated O_3 significantly reduced NPP of hardwood forests by 13–24% compared to nontreated controls. Thus, exceedances of O_3 air quality standards could mitigate or offset biomass gains from elevated CO_2 (Mohan et al. 2009) and exacerbate effects of increased temperatures and drought on forest growth in temperate hardwoods (McLaughlin et al. 2007a, b). Ozone effects may be due to reduced stomatal control of water loss. Drought alone could offset benefits associated with elevated CO_2 as shown for sweetgum (*Liquidambar styraciflua* L.) (Warren et al. 2011).

Hence, walnut's photosynthetic capacity with regard to increased CO_2 appears to be greater than average for deciduous angiosperms. Because of very limited data, however, substantial uncertainty remains regarding walnut's acclimation. Moreover, response to both CO_2 and O_3 cannot be determined given the lack of published data on O_3.

# 3 Nutrient functions

3.1 Nutrient requirements

Compared to associated species, walnut has a relatively narrow range of soil conditions on which it grows well (Thompson and McComb 1962) and requires deep, fertile soils that have a high water holding capacity (Schlesinger and Funk 1977; Williams 1990). Growth and presence are also favored on south and southwest-facing slopes (Loacker et al. 2007) but reduced on shallow, drier, more infertile soils where the genetic potential for deep rooting is not fully realized. This indicates how important root system development is to *Juglans* species.

Research findings showed positive relationships between soil nutrient content and walnut development in terms of radial growth (Ponder 1998) and biomass production (Paschke et al. 1989). In 19-year-old black walnut, estimated above-ground dry biomass (kilograms) was strongly related to total nitrate (NO_3^-, r^2=0.73) and total annual NO_3^- production (r^2=0.41, Paschke et al. 1989). In 2-year-old black walnut rootstock, fertigation treatments increased leaf nutrient content by 18% to 86% for N compared with the nontreated control after one growing season (Salifu et al. 2006). Increases in P, from 33% to 303%, and K, from 23% to 58%, were also found in comparison with the control (Salifu et al. 2006). Two additional studies on fertilization of black walnut seedlings (Nicodemus et al. 2008a, b) indicate that a mixed N source is preferred over NO_3^- or NH_4^+ alone to maximize productivity. Although walnut's nutrient requirements are high relative to other deciduous angiosperms, short-term response to fertilization can vary greatly depending upon soil conditions and type of fertilizer application (Jacobs and Seifert 2004). Black walnut's fertilization response may be lower compared to associated species such as yellow-poplar or white ash as shown for a 2-year outplanting experiment in the central USA (Jacobs et al. 2005).

3.2 Nutrient allocation and remobilization

As with other temperate hardwoods, N is essential to the early growth phase of walnut. Both C and N metabolism are related in this phase because the photosynthetic capacity of leaves depends on N content during growth (Figs. 1a, b and 3a, b). Similarly to C, walnut uses N stored in the maternal seed for taproot development (Fig. 3a). As the taproot develops from the seed in the first month of growth, N is allocated primarily to below-ground parts of seedlings, but rapidly developing aerial parts receive the majority of N during the second month of growth (Maillard et al. 1994a; Fig. 3b). Short-term nutrient uptake by roots may also be coupled to C assimilation by leaves in older walnut seedlings. Delaire et al. (2005) measured short-term (9 days) effects of a 53% increase in atmospheric [CO_2] on CO_2 uptake by shoots and nutrient uptake by roots in 2-year-old black walnut hybrids. Results showed that NO_3^-, K^+, Mg^{2+}, and Ca^{2+} uptake rates by roots were proportional to CO_2 uptake rates by shoots during the study period, with r^2 values ranging from 0.73 to 0.80. This coupling may be explained by nutrient acquisition through active transporter systems that require energy supplied by carbohydrates (Delaire et al. 2005).

a

b
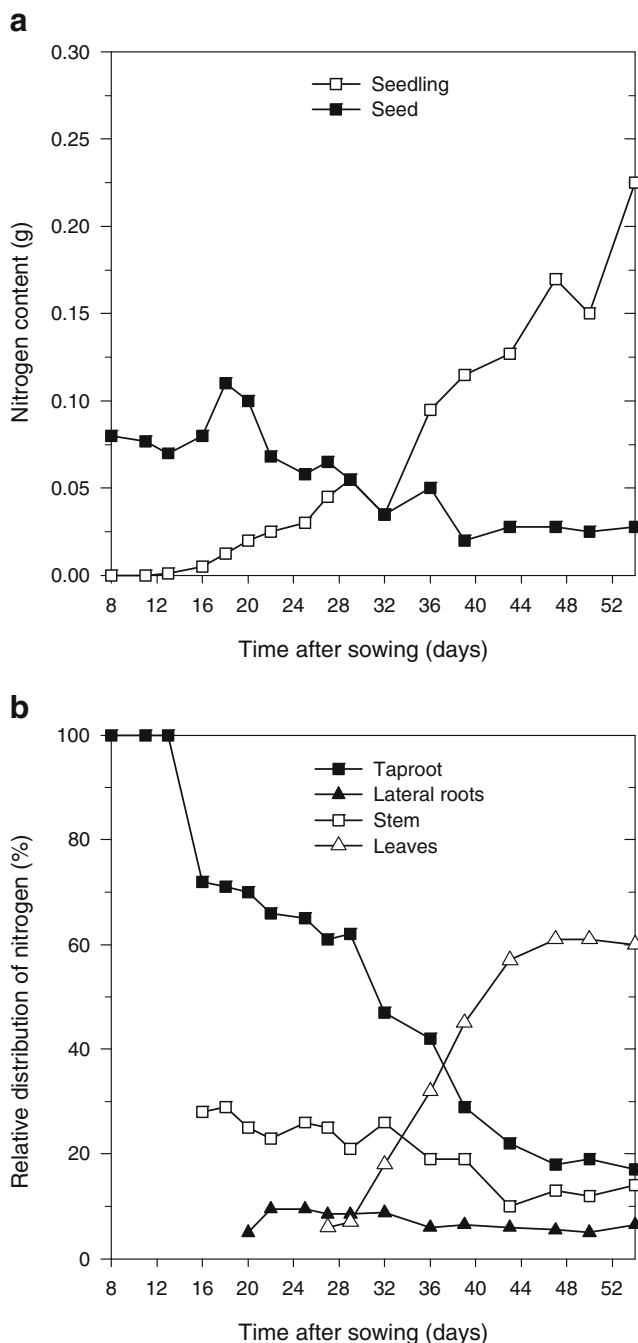
Fig. 3 Variation of nitrogen in an English walnut seedling (*J. regia* L.) and its maternal seed (**a**) and relative distribution of nitrogen in various organs of an English walnut seedling (**b**) under controlled conditions (22°C, 12 h) during the first 2 months of development. Each value is the mean obtained from the combustion of dry matter of a set of five plant samples (Maillard et al. 1994b, by permission of Oxford University Press)

Retranslocation of stored nutrients is also important in meeting demand during periods of active growth, especially in terms of N, as reported for walnut seedlings and mature trees (Deng et al. 1989; Weinbaum et al. 1994; Weinbaum and Van Kessel 1998; Frak et al. 2002b; Salifu et al. 2009).

Whereas C remobilization in tree species is largely sink-driven, N remobilization is driven by the size of the storage pool (Millard and Grelet 2010). In walnut, N derived from storage accounted for about half of the xylem sap N throughout the leaf expansion period in mature English walnut hybrids growing in the western USA (Deng et al. 1989). In 1-year-old English walnut seedlings, spring remobilization of N stored during the previous year accounted for at least 54% of total N to new shoots (Frak et al. 2002b). Salifu et al. (2009) also demonstrated the importance of retranslocation in meeting early N demand of 1-year-old black walnut seedlings growing in sand culture. Weinbaum and Van Kessel (1998) reported that 60% of annual N demand of 9-year-old English walnut hybrids was derived from redistribution of N from internal pools. The remaining 40% was met by N influx from the soil/fertilizer pool. Results from Weinbaum and Van Kessel (1998) also indicate walnut hybrids stored the majority of soil and fertilizer N absorbed and used it for new growth within 2 years of uptake. Similar N remobilization to meet nutrient demand has been shown in several tree species and shrubs (Millard and Grelet 2010), including deciduous angiosperms such as northern red oak (Salifu et al. 2008) and sugar maple (Lennon et al. 1985; Goldfarb et al. 1990).

4 Acclimation to temperature

4.1 Freezing tolerance and avoidance

Plants generally survive subzero temperatures by exhibiting freezing tolerance, such as deep supercooling, or freezing avoidance, such as stem shrinkage. Walnut can exhibit both traits. Like many associated species including northern red oak, black walnut can display deep supercooling, i.e., freezing resistance near −40°C, across its native range when fully dormant (George et al. 1977). In addition to deep supercooling, walnut can also display stem shrinkage. Améglio et al. (2001a) showed trunks of 17-year-old English walnut orchard trees shrank up to 1300 μm in diameter as air temperature fell to −10°C. Diameter expanded as temperature increased back up to 0°C. Repeated freeze–thaw cycles at increasingly colder temperatures (−2.5°C, −5°C, −7.5°C, −10°C), carried out on excised segments of twigs from orchard trees, resulted in progressive loss of diameter up to 150 μm. Stem freezing occurred between −4°C and −8°C in English walnut, and similar stem freezing values (−6°C to −9°C) were reported in black walnut (Murray and Byrnes 1975). Pronounced shrinking of the living bark due to the formation of extracellular ice is an indication of freezing avoidance (Améglio et al. 2001b) and has been shown for other temperate deciduous angiosperms like white oak (Hinckley and Bruckerhoff 1975).

Despite walnut's high freezing tolerance when fully dormant, spring frost injury appears to be important in English walnut, especially at the juvenile stage (Hemery et al. 2010; Poirier et al. 2010). Early bud break in English walnut can lead to apical bud death or shoot death during late spring frosts as shown in short-term juvenile field tests across five European countries (Fady et al. 2003). Development of freezing tolerance is thought to be related to soluble sugar accumulation (Poirier et al. 2010). In Slovenia, Crepinsek et al. (2009) analyzed the influence of increasing winter and spring air temperatures on bud break date in English walnut. Compared to the 1984–1990 period, mean air temperature from January to April increased by 0.9°C during the 2000–2006 period and bud break occurred 3–7 days earlier. By 2060, phenological models suggest bud break could be advanced up to 4 weeks, thus increasing frost hazard. Repeated freeze–thaw events can also lead to embolism, a phenomenon that has been the topic of many experiments with English walnut.

4.2 Acclimation to freezing temperatures and embolism recovery

Also termed cavitation, embolism is the formation of air bubbles in xylem vessels that can be caused by attainment of threshold negative hydrostatic pressures (tension) during drought and winter freezing events. Freeze–thaw cycles also cause embolism when air dissolved in xylem water is released from solution during ice formation. Walnuts are semi ring-porous species with large vessel diameters, which are of intermediate width compared to larger ring-porous species (northern red oak) and smaller diffuse-porous species (sugar maple). Ring-porous or semi ring-porous species are more susceptible to cavitation of xylem water columns during winter compared to diffuse-porous species or gymnosperms (Lechowicz 1984; Sperry et al. 1994). Tree species susceptible to water deficits are also more prone to cavitation (Tyree and Cochard 1996). Embolism effectively renders xylem conduits non conductive. This loss may be permanent or repair may occur so that hydraulic conductivity fully recovers (Améglio et al. 2002).

Repair in walnut species involves the development of positive hydrostatic pressures in roots and stems. In English walnut, root pressures were generated at temperatures above 15°C in autumn and spring, while stem pressures were involved at temperatures below 5°C in winter (Ewers et al. 2001). The greatest root pressures tend to occur in spring to help remove winter embolism that may have occurred in xylem vessels. Many other deciduous angiosperms such as European beech (Fagus sylvatica L.) develop positive xylem pressures in early spring, but not in winter (Cochard et al. 2001). Pressure apparently results from influx of carbohydrates into xylem from the symplast

of neighboring tissues, a process that is correlated with seasonal changes in soil and air temperature in English walnut (Améglio et al. 2001c, 2004; Fig. 4). Sucrose demand by developing buds, leaves, and shoots provides a sink needed to move carbohydrates into the xylem (Decourteix et al. 2008; Bonhomme et al. 2010). This positive xylem pressure refills vessels, which regain hydraulic function (Améglio et al. 2002). Secondarily, new xylem is formed each spring, providing additional conduits for axial water flow. This mechanism is common to all plant species with secondary cambium (Cochard et al. 2001). Experiments by Alves et al. (2004, 2007) found that plasma membrane H^+-ATPase plays an important role in the uptake of carbohydrates from xylem vessels during growth resumption in English walnut. Sucrose and hexose transporters (JrSTU1, JrHT1, JrHT2) involved in parenchyma cells of xylem vessels were also identified in English walnut (Decourteix et al. 2006, 2008).

4.3 Heat stress

In terms of heat stress, the critical leaf temperature inducing photochemistry damage appears to be remarkably similar (~47.0°C) among many deciduous angiosperms of western Europe (Dreyer et al. 2001). Using chlorophyll a fluorescence measurements, trends showed values of maximal carboxylation rate (V_{cmax}, micromoles of CO_2 per square meter per second) and light-saturated electron transport (J_{max}, micromoles of electrons per square meter per second) at 25°C were the lowest in English walnut (63.6 and
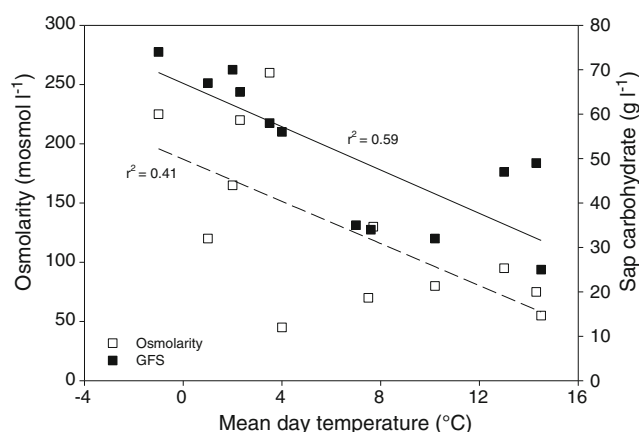
Fig. 4 Relationships between xylem sap osmolarity (milliosmoles of solute per liter of solution, $r^2=0.41$) or sap sugar concentration (GFS glucose + fructose + sucrose, $r^2=0.59$) and mean daily air temperature on 12 dates from November 1996 to March 1997. Xylem measurements were taken on excised, 1-year-old twigs of walnut (J. regia L. cv. Franquette scions on wild walnut rootstocks) from a 15-year-old walnut orchard. Each value represents the mean of nine twigs. Mean air temperature was computed as the mean of the minimum and maximum air temperatures recorded for each date (Améglio et al. 2004, by permission of Oxford University Press)

102.3 $\mu mol\ m^{-2}\ s^{-1}$, respectively) compared to other species including sycamore maple (*Acer pseudoplatanus* L.), pedunculate oak, and sessile oak (*Quercus petraea* Matt. Liebl.). In walnut, the highest V_{cmax} values were attained at 36.6°C, in the lower range compared to other species. This is in contrast to J_{max}, where the temperature of 37.3°C was at the high end of the range. Species differences in V_{cmax} could be due to intrinsic differences in Rubisco, while changes in J_{max} could be due to thylakoid membrane properties (Dreyer et al. 2001).

There can be considerable variation in both V_{cmax} and J_{max} in walnut seedlings: Le Roux et al. (1999a) reported a range of V_{cmax} from 20 to 69 $\mu mol\ m^{-2}\ s^{-1}$ and J_{max} from 45 to 178 $\mu mol\ m^{-2}\ s^{-1}$ in sun and shade leaves. Values reported by Dreyer et al. (2001) also compare favorably to mean V_{cmax} (47.0 $\mu mol\ m^{-2}\ s^{-1}$) and J_{max} (104.0 $\mu mol\ m^{-2}\ s^{-1}$) values reported for 19 temperate deciduous angiosperms by Wullschleger (1993).

5 Water relations

Plant water relations may be used to describe a plant's characteristics in terms of drought or flood tolerance. There is some evidence to suggest walnut may be flood intolerant (Mapelli et al. 1997; Dudek et al. 1998; Winter et al. 2009), but this aspect of water relations will not be covered in more detail due to the small number of experiments conducted on the subject compared to drought tolerance.

5.1 Drought tolerance

Based on Kramer's (1983) terminology, plants can be classified based on their capacity to avoid or tolerate drought. Drought avoidance refers to desert plants that avoid drought periods by completing their life cycle prior to the onset of drought. Hence, most other plants, including walnut, can be characterized in terms of drought tolerance. Tolerance is divided into desiccation avoidance and desiccation tolerance.

From the literature, black walnut has an extensively deep rooting habit (Williams 1990; Pallardy and Rhoads 1993) that allows it to maintain higher predawn leaf water potential (Ψ_{pd}) by extracting deep soil moisture unavailable to associated species like white oak (Hinckley et al. 1979; Martin et al. 1980; Lucier and Hinckley 1982; Ginter-Whitehouse et al. 1983). Root growth and number of growing roots, however, are still reduced by water deficits as reported by Kuhns et al. (1985).

Black walnut and English walnut also display high stomatal sensitivity to humidity, i.e., stomatal control of transpirational water loss in seedlings (Ni and Pallardy 1990, 1992; Parker and Pallardy 1991) and mature trees

(Lucier and Hinckley 1982; Loewenstein and Pallardy 1998a; Daudet et al. 1999). Black walnut limits water loss in response to high vapor pressure gradients (Lucier and Hinckley 1982; Green 1993). Stomatal closure may regulate water tension in the leaf rachis xylem (P_{rachis}) in English walnut (Cochard et al. 2002). Mechanisms by which stomata can sense changes in P_{rachis} to regulate g and prevent embolism are still unknown, but soil Ψ or ABA production by roots was ruled out based on findings from Cochard et al. (2002). The signaling mechanism may reside in the leaf mesophyll itself. This is in contrast to findings from other studies with black walnut (Loewenstein and Pallardy 1998a, b, 2002) that suggest xylem sap [ABA] could act as a signal to regulate g during periods of water deficits.

Contrary to most associated species, walnut is well-known for exhibiting leaf abscission in periods of drought (Parker and Pallardy 1985a; Ni and Pallardy 1991; Pallardy and Rhoads 1993; Tyree et al. 1993). Ni and Pallardy (1991) found that 3-month-old black walnut seedlings placed in a growth chamber stopped CO_2 assimilation and leaflets began senescing at Ψ values of −2.2 MPa or less. Tyree et al. (1993) also reported leaf shedding at similar Ψ values in 1-year-old English walnut seedlings subjected to drying cycles. Given walnut's relatively short period of active photosynthesis, leaf abscission reduces the amount of C that can be accumulated in fall and remobilized in spring.

The deep root system, stomatal sensitivity to humidity, and drought-induced leaf abscission habit suggest that walnut is comparatively sensitive to water deficits, with physiological responses being reflective of this sensitivity. Moreover, all three of these features are desiccation avoidance mechanisms that act to maintain high leaf water content. Failure to do so is reflected in comparatively large reductions in photosynthetic capacity (Davies and Kozlowski 1977; Hinckley et al. 1979) and likely drought-induced embolism (Cochard et al. 2002). Even in the absence of leaf abscission, drought may decrease the amount of accumulated C during late summer and fall, thus lowering winter frost resistance and embolism repair. Because walnut bud break occurs relatively late, winter embolism repair also serves a critical role in walnut's water relations by restoring hydraulic conductivity at bud break. This allows for rapid primary growth without prior need to build new secondary tissues. Without this repair mechanism, walnut's susceptibility to drought would increase and growth rate could be severely reduced.

To better illustrate walnut's desiccation avoidance, Davies and Kozlowski (1977) used a soil drying cycle to investigate effects of water deficits on 2- and 3-year-old potted seedlings of six woody angiosperms growing in controlled environments. As drought stress increased and leaf Ψ reached −2.5 MPa, relative rates of A rapidly

dropped near 0% (Fig. 5). Compared to sugar maple and American elm (*Ulmus americana* L.), black walnut was the only species that did not recover from drought, exhibiting "leaf yellowing and senescence symptoms as soil water became limiting" (Davies and Kozlowski 1977). Black walnut was ranked as having the lowest ability to photosynthesize under drought stress compared to white oak, northern red oak, and sugar maple (Hinckley et al. 1979). Using electrolyte leakage measurements, Martin et al. (1987) showed that leaf desiccation tolerance acclimation was poorly developed in black walnut compared to northern red oak and white oak.

5.2 Other leaf osmotic adjustments

Walnut exhibits other leaf osmotic adjustments that can vary greatly among families (Parker and Pallardy 1985a, b). Such adjustments include increased water-use efficiency (WUE; micromoles of CO_2 per mole per H_2O) and leaf hydraulic conductance (K_{leaf}; millimoles of H_2O per second per megapascal). These may also be regarded as desiccation avoidance mechanisms, although the relationship is not as evident as rooting habit, stomatal closure, or leaf abscission. Picon-Cochard et al. (2001) used labeling techniques to study competition of rye grass and drought on photosynthetic parameters of 3-month-old English walnut seedlings. Walnut displayed much higher WUE (41%) than rye (*Lolium perenne* L.) grass when grown separately. Drought was found to increase WUE by nearly 40% in English walnut seedlings when growing with rye grass
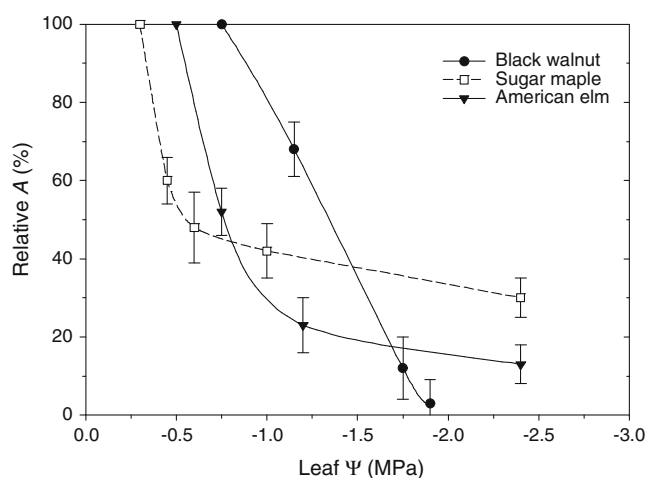
Fig. 5 Influence of drought as measured by leaf water potential (Ψ, megapascals) on the relative net photosynthesis (*A*, in percent) of 3-year-old black walnut (*J. nigra* L.) and sugar maple (*A. saccharum* Marsh.) seedlings and 2-year-old American elm (*U. americana* L.) seedlings. Potted plants were subjected to a soil drying cycle and compared to seedlings growing in unstressed environmental conditions. With kind permission from Davies and Kozlowski (1977) and Springer Science + Business Media, Fig. 2

competition, but not in the pure walnut treatment. During initial drought stress, several deciduous angiosperms can display transient increases in WUE, such as northern red oak and sugar maple (Ni and Pallardy 1991). Black walnut, however, can maintain higher WUE than most associated species until severe water deficits occur, eventually decreasing WUE (Ni and Pallardy 1991). Cochard et al. (2007) found that leaves from mature English walnut trees can quickly change K_{leaf} in response to light and temperature. Furthermore, these changes can be explained by regulation of aquaporins (*JrPIP2,1* and *JrPIP2,2*), proteins located in the plasma membrane that allow transport through cell membranes. Results indicate that water flow through walnut leaves under high light followed a symplastic pathway and was influenced by increases in the density of aquaporins in the cell membrane. In the dark, however, the apoplastic route was prevalent and influence of aquaporins was limited. Aquaporins are also involved in walnut embolism recovery (Sakr et al. 2003).

6 Potential effects of climate change

Regional climate change projections from the Intergovernmental Panel on Climate Change (IPCC) were used to describe potential changes in temperature and precipitation in the distribution areas of both species (Christensen et al. 2007). Changes refer to the difference between the 2080–2099 and 1980–1999 periods and were based on the IPCC's A1B scenario that describes the twenty-first century as a "world of very rapid economic growth, a global population that peaks in mid-century and rapid introduction of new and more efficient technologies" that are balanced between fossil and non-fossil energy resources (Nakicenovic et al. 2000). In North America and northern Europe, mean annual temperature and precipitation are expected to increase (Table 2). Moreover, extreme climatic events, such as storms, floods, and droughts, may occur more frequently and become more harmful in northern Europe (Lindner et al. 2010). For southern Europe and the Mediterranean, mean annual temperature is expected to rise while precipitation is expected to decrease (Table 2). Risk of summer drought is likely to increase in these regions (Christensen et al. 2007), including western Europe (Bréda et al. 2006). In terms of elevated CO_2, concentrations are projected to increase to at least 486 μmol mol^{-1} by 2100 compared to preindustrial values of 280 μmol mol^{-1} (Nakicenovic et al. 2000).

This information, combined with many of the previously addressed topics, can provide insight on climate change impacts on walnut growth. This insight is especially relevant in wild or extensively managed areas where nutrient supply is limiting. The magnitude of change in

temperature is much greater than potential changes in precipitation (Table 2). There are concerns that these conditions may increase evapotranspiration rates (Lemprière et al. 2008; Huntington et al. 2009) and make forest tree species more susceptible to drought. As such, walnut may be at a disadvantage due to its susceptibility to water deficits, especially where drought events are predicted to occur more frequently. In the central USA, water deficits early in the growing season may be the most important factor limiting growth of black walnut on upland sites (Dudek et al. 1998). This could be particularly important for establishment and growth of regeneration because research findings suggest seedlings may be more intolerant of drought than mature trees.

Walnut may also be more susceptible to late spring frost injury and embolism due to increased freeze–thaw events, as shown in the temperature section. Moreover, development of freezing tolerance and embolism recovery in walnut are both related to soluble sugar accumulation (Decourteix et al. 2008; Bonhomme et al. 2010; Poirier et al. 2010). Thus, an increase in summer drought or heat stress may also increase spring frost hazard due to a reduction in accumulated C and stored N during the previous growing season. Some of the lowest annual diameter growth rates reported in English walnut were associated with exceptionally cool temperatures in late spring and early summer (Winter et al. 2009). Certain walnut growing regions could be impacted according to current predictions of future climates, such as the western USA (Allen et al. 2010) and portions of Europe under Mediterranean and temperate continental climates (Lindner et al. 2010). There is already some modeling evidence suggesting climate change may lower chilling requirements in California, making walnut more vulnerable to frost-induced embolism in early spring (Baldocchi and Wong 2008) and pest attacks (Luedeling et al. 2011). Similarly, phenological models indicate that increasing spring temperatures may advance bud break by up to 4 weeks in central Europe, thus increasing spring frost hazard (Crepinsek et al. 2009).

There is also evidence suggesting walnut growth and distribution may remain stable or increase in the twenty-first century. This evidence is based on larger-scale studies. For traditionally cold walnut growing regions with mean annual temperature of 7–8°C, projected increases in temperature that provide milder winters may actually increase walnut establishment as reported for English walnut in inner Alpine valleys of Austria (Loacker et al. 2007). These findings indicate that areas that are currently considered cold for walnut growth may see increased establishment and growth depending upon the rate of temperature increase and the frequency and severity of extreme climatic events. Another large-scale study of 130 tree species in North America showed black walnut's climate-envelope area may not be drastically reduced by 2100 (McKenney et al. 2007). Under a scenario where populations can fully migrate into their future climate habitat, black walnut's distribution was projected to shift northward by 8.2° latitude (~900 km) compared to 6.4° (~700 km) for all species combined. This placed black walnut 15th out of 130 species in terms of northward shift but still behind several associated deciduous angiosperms: sugar maple, northern red oak, white ash, and white oak (McKenney et al. 2007). Under a scenario where populations survive only in areas that overlap their current range, black walnut's predicted northward shift was the same as the overall mean of 3.0° (~330 km). The actual shift is likely to be found between these two extremes. In addition to these studies, productivity gains associated with increased atmospheric CO_2 in walnut appear to be greater than average, but there are very few published results for walnut, combined with a lack of data on negative effects of elevated O_3.

7 Future research needs

Overall, some studies tend to indicate walnut could be negatively impacted by climate change, while others do

Table 2 Median annual and seasonal (summer, winter) temperature and precipitation projections for various regions where walnuts occur

Species	Climate	Region	Temperature (°C)			Precipitation (%)		
			Sum	Win	Ann	Sum	Win	Ann
Black walnut	Humid continental	Eastern North America	3.3	3.8	3.6	1	11	7
(*Juglans nigra*)	Humid subtropical	Central North America	4.1	3.5	3.5	−3	5	3
	Mediterranean	Western North America	3.8	3.6	3.4	−1	7	5
English walnut	Temperate oceanic	Northern Europe	2.7	4.3	3.2	2	15	9
(*Juglans regia*)	Temperate continental, Mediterranean	Southern Europe and the Mediterranean	4.1	2.6	3.5	−24	−6	−12

Values represent the difference between the 2080–2099 and 1980–1999 periods. Full details of climate change scenario projections can be found in Christensen et al. (2007)

ann annual, *sum* summer, *win* winter

not. There is also considerable uncertainty regarding the magnitude of potential climate change effects, from growth and development of individual trees to survival and distribution patterns of the genus. We identified a number of areas that could help address some of this uncertainty. Quantifying walnut's response to elevated CO_2 and O_3 would be essential to determine potential impacts on productivity. We found few experiments investigating the effects of heat stress, which may be critical to growth and survival under warmer temperatures and increased frequency of extreme climatic events. We believe that research investigating a combination of environmental factors (temperature, CO_2, O_3, N, water) would provide a better understanding of integrated stress response of walnut. In our view, patterns of C and N allocation and remobilization during periods of environmental stress warrant further investigation given the importance of these mechanisms. Additional research in these areas would help increase our understanding of the fundamental processes related to physiological acclimation to climate change.

Flooding responses have received little attention compared to the impacts of water deficits; more research is needed to elucidate flooding effects on ecophysiological processes of walnut and their subsequent impact on growth. Nutrient processes have been largely directed at N; experiments that examine other macronutrients that are essential for growth and survival, such as P and K, would enhance depth in knowledge of walnut nutrient dynamics.

At a larger scale, we recommend investigations into walnut's natural distribution across a gradient of physiographic and climatic features, e.g., altitude, temperature, precipitation, drainage, soil fertility, slope, aspect. This would help connect ecophysiological responses with long-term forest development and stand dynamics.

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