Chapter 10
Relationships Between Tree Height and Carbon Isotope Discrimination

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Abstract Understanding how tree size impacts leaf- and crown-level gas exchange is essential to predicting forest yields and carbon and water budgets. The stable carbon isotope ratio ($\delta^{13}C$) of organic matter has been used to examine the relationship of gas exchange to tree size for a host of species because it carries a temporally integrated signature of foliar photosynthesis and stomatal conductance. The carbon isotope composition of leaves reflects discrimination against ^{13}C relative to ^{12}C during photosynthesis and is the net result of the balance of change in CO_2 supply and demand at the sites of photosynthesis within the leaf mesophyll. Interpreting the patterns of changes in $\delta^{13}C$ with tree size are not always clear, however, because multiple factors that regulate gas exchange and carbon isotope discrimination (Δ) co-vary with height, such as solar irradiance and hydraulic conductance. Here we review 36 carbon isotope datasets from 38 tree species and conclude that there is a consistent, linear decline of Δ with height. The most parsimonious explanation of

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this result is that gravitational constraints on maximum leaf water potential set an ultimate boundary on the shape and sign of the relationship. These hydraulic constraints are manifest both over the long term through impacts on leaf structure, and over diel periods via impacts on stomatal conductance, photosynthesis and leaf hydraulic conductance. Shading induces a positive offset to the linear decline, consistent with light limitations reducing carbon fixation and increasing partial pressures of CO_2 inside of the leaf, p_c at a given height. Biome differences between tropical and temperate forests were more important in predicting Δ and its relationship to height than wood type associated with being an angiosperm or gymnosperm. It is not yet clear how leaf internal conductance varies with leaf mass area, but some data in particularly tall, temperate conifers suggest that photosynthetic capacity may not vary dramatically with height when compared between tree-tops, while stomatal and leaf internal conductances do decline in unison with height within canopy gradients. It is also clear that light is a critical variable low in the canopy, whereas hydrostatic constraints dominate the relationship between Δ and height in the upper canopy. The trend of increasing maximum height with decreasing minimum Δ suggests that trees that become particularly tall may be adapted to tolerate particularly low values of p_c.

1 Introduction

Understanding how tree size impacts gas exchange is essential to predicting forest yields, carbon budgets, hydrology, and regional climate, each of which has scientific, economic, and policy impacts throughout the globe (IPCC 2007; Bonan 2008). The stable carbon isotope ratio ($\delta^{13}C$) of organic matter has been frequently used to examine the relationship of gas exchange to tree size (Ryan et al. 2006) because it carries a temporally integrated signature of foliar photosynthesis and stomatal conductance (Ehleringer 1993; Seibt et al. 2008). This tool works because carbon isotope discrimination (Δ) against ^{13}C relative to ^{12}C during photosynthesis is driven by the net effect of CO_2 supply and demand on the CO_2 mole fraction at the sites of photosynthesis within the mesophyll (Farquhar et al. 1982). Interpretation of the patterns of Δ with tree size is not always clear, however, because multiple factors that regulate gas exchange and Δ co-vary with height, such as solar irradiance (Farquhar et al. 1982; Ehleringer et al. 1986) and hydraulic conductance (Waring and Silvester 1994). In the last two decades a relatively large volume of data regarding the relationship between Δ and tree height has been published; however, no synthetic review has yet been undertaken. Such a review may allow improved interpretation of size–Δ relationships and hence better utilization of $\delta^{13}C$ as a tool to understand adjustments in gas exchange as trees grow larger. Our objective was to review published datasets along with five additional, unpublished datasets on Δ–size patterns in relation to environmental and physiological factors that change as trees become larger. In addition, we examined a case study of the gas exchange characteristics of short and tall mountain beech (*Nothofagus solandrii*) trees to examine potential mechanisms driving Δ patterns with height.

A brief review of the dependence of tissue $\delta^{13}C$ on gas exchange is required to provide a hypothesis framework for the size-related factors that may influence Δ. The two stable isotopologues (molecules that differ only in their isotopic composition) of CO_2, $^{13}CO_2$ and $^{12}CO_2$ represent approximately 98.9% and 1.1% of atmospheric CO_2, respectively. Discrimination against $^{13}CO_2$ during photosynthesis arises mainly from gaseous diffusion from the atmosphere through the stomatal pores to the outer mesophyll cell walls (4.4‰, *a* in Eq. 10.1), and carboxylation by the enzyme Rubisco (~27‰, *b*). Discrimination associated with liquid diffusion across membranes to the sites of carboxylation in the chloroplasts is typically lumped into parameter *b* (Brugnoli and Farquhar 2000; Bickford et al. 2010). These processes are captured in Eq. 10.1 (Farquhar et al. 1982):

$$\Delta \approx a + (b - a) \cdot \frac{p_c}{p_a} \tag{10.1}$$

where p_c and p_a are the chloroplast and atmospheric partial pressures of CO_2, respectively (Hultine and Marshall 2000; Seibt et al. 2008). Thus, anything that affects p_c affects Δ. This is a simplified representation of the processes that influence Δ but it provides an initial hypothesis framework.

Gas exchange characteristics may change as trees become larger due to size-dependent variation in environmental and structural factors and their interactions, such as changes in light availability, hydraulic conductance, and carbon allocation (e.g., Yoder et al. 1994; Gower et al. 1996; Ryan and Yoder 1997). Some traits, such as leaf mass per area and sexual maturation, vary with meristem age independently of size (Bond 2000; Bond et al. 2007; Greenwood et al. 2008; Thomas 2011); however, developmental changes in gas exchange are driven by tree size rather than age (Day et al. 2002; Mencuccini et al. 2005; Bond et al. 2007; Steppe et al. 2011). Thus, we use the term size rather than age throughout this paper (McDowell et al. 2005). We know from Fick's law that photosynthetic assimilation (*A*) and conductance to CO_2 from the atmosphere to chloroplast (g_c, which includes stomatal g_s, and internal g_i) control p_c when p_a is relatively stable:

$$p_c \approx p_a - \frac{A}{g_c} \tag{10.2}$$

The interaction of tree size, physiology (Eqs. 10.1 and 10.2), and some environmental variables was originally conceptualized in a seminal paper by Francey and Farquhar (1982).

One important size-related environmental change is increased shading within tree crowns (Francey et al. 1985; Ehleringer et al. 1986; Hanba et al. 1997; Carswell et al. 2000; Parker et al. 2002; Poorter et al. 2005; Lloyd et al. 2009) which raises p_c because *A* declines via reduced light interception. This change in the light environment occurs within the height profile of individual trees within closed-canopy forests, but does not occur at the tops of canopy-dominant trees or in open-grown trees. Other environmental factors influencing p_c and Δ that may change during forest growth include atmospheric CO_2 concentration (Medina and Minchin 1980; Sternberg et al. 1989), humidity, temperature and wind speed (Baldocchi et al. 2002), and water and nutrient availability (Yoder et al. 1994; Gower et al. 1996; Magnani et al. 2000; Niinemets 2002; Martínez-Vilalta et al. 2007a).

There are numerous structural factors that may impact Δ as trees grow. Plant size directly impacts gas exchange through the relationship of hydraulic supply and demand (e.g. Meinzer and Grantz 1990; Mencuccini and Comstock 1999) including impacts on hydraulic conductance associated with increasing soil-to-leaf pathlength (above and belowground) (Yoder et al. 1994; Mencuccini and Grace 1996a; Ryan and Yoder 1997; Phillips et al. 2002; Mencuccini 2003). This relationship can be conceptualized via Darcy's law (Whitehead 1998):

$$g_c \approx \frac{k_s A_s \left(\psi_l - \psi_s\right)}{h A_l \eta D} \tag{10.3}$$

in which k_s is specific conductivity of the xylem, A_s and A_l are sapwood and leaf area, respectively, Ψ_l and Ψ_s are leaf and soil water potential, respectively, η is the viscosity of water, and D is vapor pressure deficit. We note that the original formulations of this model used g_s to represent stomatal conductance to water vapor, which is equivalent to g_c after correction for the 1.6 higher diffusivity of water vapor than CO_2. Height (h) is the most easily and commonly measured component of the pathlength, although it is not the only component. The use of height as a surrogate for pathlength can mislead people to think height alone is a driver of reduced gas exchange in trees, when in fact much of the increase in pathlength and hydraulic resistance is located in roots and branches (Magnani et al. 2000; Sperry et al. 2002; Martínez-Vilalta et al. 2007b). Nonetheless, if pathlength increases and all other components stay relatively constant, then Eq. 10.3 reduces to $g_c = c*1/h$ (where c is a constant), which takes the shape of a non-linear decline in g_c with pathlength. Both hydraulic and stomatal conductances follow this relationship (Mencuccini and Grace 1996b; McDowell et al. 2002a; Niinemets 2002; Schäfer et al. 2000). Thus far it has been shown that many structural factors vary with increasing h to minimize its impact on g_c as trees grow larger, but that these homeostatic adjustments fail to completely offset the negative impact of h on g_c (McDowell et al. 2002a, b; Mencuccini 2003), in part due to requirements to protect xylem from irreversible embolism (Domec et al. 2008). Height itself may be restricted in a homeostatic manner, i.e. reduced height growth facilitates maintenance of g_c above critically low thresholds, even for plants with short maximum heights (Addington et al. 2006; Ryan et al. 2006). Equation 10.3 is based on the premise that irreversible embolism is avoided in part through constraining g_s during periods of water limitation, and does not include variation in light or leaf properties, for example, so it provides only an approximate hypothesis about how gas exchange varies with size.

The interactive impacts of irradiance and pathlength on Δ were demonstrated by Waring and Silvester (1994), who sampled foliage from a range of branch lengths

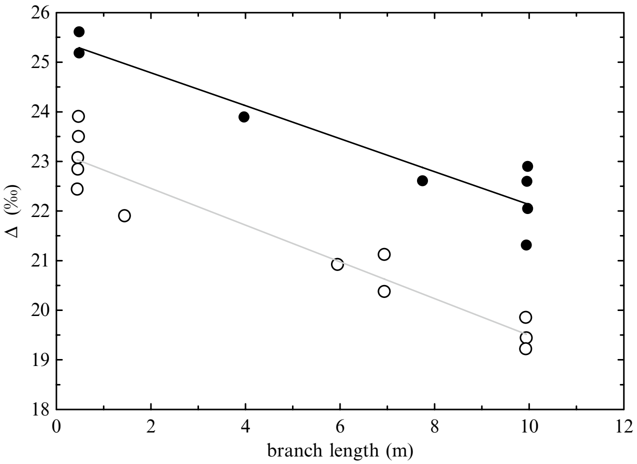

Fig. 10.1 The relationship of Δ calculated from foliar $\delta^{13}C$ to branch length on shaded (*closed circles*) and sunlit (*open circles*) sides of *Pinus radiata* trees. The regression lines are sunlit $\Delta = -0.37 \cdot \text{length (m)} + 23.2$ ($r^2 = 0.92$, $p < 0.001$) and shade $\Delta = -0.33 \cdot \text{length (m)} + 25.4$ ($r^2 = 0.89$, $p < 0.001$) (Recreated from Waring and Silvester 1994)

on sunny and shady sides of open-grown *Pinus radiata* trees (Fig. 10.1). Consistent with Eqs. (10.1–10.3), Δ declined with decreasing p_c due to increased *A* at higher irradiance, and decreased g_c with longer branch lengths. Other structural and physiological responses to increased tree size that can impact Δ include increases in leaf thickness (Vitousek et al. 1990; Bond et al. 1999; Hanba et al. 1997; Koch et al. 2004; Ishii et al. 2008; Ambrose et al. 2009; Ishii 2011) and hence decreasing g_i (Warren and Adams 2006), although correlations between g_i and leaf thickness are not always observed (Terashima et al. 2005). This morphological response is commonly thought to be adaptive to the light environment, although it also driven by the gravitational constraint on leaf water potential (0.01 MPa m^{-1}) and subsequent impacts on turgor during leaf expansion (e.g. Marshall and Monserud 2003; Woodruff et al. 2004; Cavaleri et al. 2010; Woodruff and Meinzer 2011). Foliar nitrogen content may increase with light availability within crowns (Bond et al. 1999; Duursma and Marshall 2006; Lloyd et al. 2009), which could increase *A* and hence reduce Δ via increased photosynthetic capacity. This is not observed between fully sunlit trees of different heights, however (e.g. Mencuccini and Grace 1996b; Ryan et al. 1997; McDowell et al. 2002a).

It is no surprise that mixed interpretations of the variation in Δ with tree height arise given the large number of environmental and structural factors that change with tree growth. Therefore, we reviewed all available data sets that provided both Δ and *h*, with consideration of these other factors when possible, in hopes of better understanding how Δ, and hence gas exchange, varies with tree size. This review includes woody trees and shrubs from any regions that we could find in the literature.

Based on Fig. 10.1, Eqs. 10.1–10.3, and the assumption that plants allocate their carbon and nutrient capital optimally to maximize whole-plant A while avoiding irreversible embolism (Bloom et al. 1985; Mencuccini 2003; Buckley and Roberts 2006; Lloyd et al. 2009), we hypothesized that a decline in Δ with h, as h approaches its site- and species-specific maximum, is universal regardless of climate or species. In such an observational analysis it is impossible to mechanistically partition the effects of each of the above-mentioned drivers on Δ. Open- and closed canopy trees were sampled together in some of the studies, however, allowing us to test the hypothesis that shade causes a positive offset of the foliar Δ/h relationship relative to sunlit foliage. To further examine mechanisms, we included a detailed case study on short and tall (maximum local height) mountain beech (*Nothofagus solandri*) trees as a test of the role of gas exchange characteristics in Δ/h patterns.

2 Methods

2.1 *Case Study*

We measured gas exchange (g_s, and A), Ψ_1 and foliar and wood $\delta^{13}C$ for two tree sizes (average heights 4.3 and 11.2 m) in a *Nothofagus solandri* stand at 1,300 m elevation at Craigieburn Forest Park in New Zealand. To examine if patterns found in the stand at 1,300 m varied with climate, we also sampled foliar $\delta^{13}C$ from canopy tops of *Nothofagus solandri* trees at five additional sites distributed along an elevation gradient from 800 to 1,250 m above sea level. Cragieburn Forest Park is located in central South Island, New Zealand (43°15′S, 171°35′E). Mountain beech forest occurs as a mono-specific forest from valley bottoms at 650 m to tree line at 1,400 m elevation. At 914 m elevation, mean annual temperature is 8.0°C, mean annual precipitation is 1,447 mm, and mean annual radiation is 4,745 MJ/m^2 (McCracken 1980). At 1,240 m elevation, annual precipitation was estimated to be 1,700 mm and mean annual temperature 6°C (Tate et al. 2000). The soil was formed from mixed greywacke loess and colluvium over shattered rock, and was a fine sandy, mixed, frigid, Andic Dystrochrept called Bealey silt loam (Tate et al. 2000). Characteristics of forest stands similar to those sampled in this study are described by Tate et al. (2000), Davis et al (2003), and Allen et al. (1997).

The response of A and g_s to D was measured at the tops of the *Nothofagus* trees using a portable gas exchange system (LI-COR 6400, LI-COR Inc., Lincoln, NE, USA). Measurements were taken with C_a = 385 ppm, photosynthetically active radiation >1,000 μmol m^{-2} s^{-1}, and ambient humidity to allow for D to increase as temperature increased throughout the day. Because tree stomata are slow to respond, and humidity in the cuvette reflects an increase over ambient from transpiration, we calculated D from leaf temperature (LI-COR's energy balance calculation) and ambient humidity measured with a sling psychrometer or from a weather station 1 km distant. Gas exchange was measured on four trees of each size class and three to seven shoots per tree. Where possible the same shoots were measured periodically throughout the day. Measurements were made over a 2-week period, and a hydraulic lift was used to reach the canopy top for sampling. Leaf water potential was measured periodically on adjacent shoots with a Scholander pressure chamber (PMS Instrument Company, Albany, OR, USA). Leaf-specific hydraulic conductance (K_l) was calculated as transpiration divided by $\Psi_l - \Psi_s$, where Ψ_s was pre-dawn Ψ_l (Phillips et al. 2002).

Foliage for analysis of $\delta^{13}C$ and nitrogen was collected from canopy tops at the 1,300 m site, and along the elevation gradient. For the elevation gradient, we also sampled from two height classes: trees about 4 m in height, and trees >11 m in height. Maximum tree height increased as elevation decreased, from ~11 m at 1,300 m elevation to ~18 m at 800 m elevation. Wood was sampled for $\delta^{13}C$ either from disks from harvested trees (short trees) or increment cores (tall trees). Foliage and wood samples were dried at 65°C, ground, and analyzed for $\delta^{13}C$ composition using a an isotope ratio mass spectrometer (Europa Scientific 20/20) interfaced to a Dumas elemental analyser (Europa Scientific ANCA-SL, Europa Scientific Ltd., Crewe, UK). Nitrous oxide was removed by gas chromatography and corrections for ^{17}O were done for all runs (Craig 1957). Isotope ratios were presented relative to Vienna PeeDee belemnite carbonate standard (*VPDB*), calibrated against a certified secondary source from the Australian Commonwealth Scientific and Research Organization, Canberra, Australia.

We corrected the isotopic results for elevation impacts on CO_2 partial pressure (Hultine and Marshall 2000; Warren et al. 2001; Körner 2007; McDowell et al. 2010). Though this effect is minor, it is relatively straightforward to correct for when elevation and temperature are known. We used local mean temperature data for each site to calculate the drawdown of CO_2 partial pressure between the atmosphere and chloroplast ($p_a - p_c$, Pa, Hultine and Marshall 2000).

2.2 Global Patterns

We examined the relationship of Δ to h at the global scale through a literature review along with an additional five unpublished data sets of trees, shrubs, angiosperms, gymnosperms, and across all possible regions and latitudes. We searched the literature for papers that included figures or tables with both height and either $\delta^{13}C$ or Δ data from foliage or stemwood to maximize the breadth of our investigation. A few publications were excluded because height was provided qualitatively (i.e. low and high) rather than with quantifiable units (i.e. meters), and therefore could not be analyzed quantitatively. All stemwood samples were collected from breast height and most used data from the most recent year of growth. For graphical data we digitized the figures to generate numerical datasets (ImageDIG *Version 2.0.7*, SciCepts Engineering, Chiangmai, Thailand). Comparison of the digitized numerical output to known values using a somewhat fuzzy pdf copy of data from Yoder et al. (1994) showed strong correspondence (digitized $\delta^{13}C = 0.99 \cdot$ true $\delta^{13}C + 0.03$, $r^2 = 0.99$, $p < 0.001$). A slightly weaker relationship was observed using a clear pdf of Barnard and Ryan (2003) to actual data (digitized $\delta^{13}C = 0.91 \cdot$ true $\delta^{13}C - 3.2$, $r^2 = 0.99$, $p < 0.001$), with the error attributed to the loss of eight data points due to overlapping points that could not be discerned. Thus, large datasets with overlapping clouds of points may have lower accuracy than data sets with fewer points.

Our primary form of analysis was regression of Δ versus h. The slope of this relationship was used to compare the sensitivity of Δ to h across studies (e.g. McDowell et al. 2002b). The theoretical regression should be non-linear according to the simplest version of Darcy's law ($\Delta = 1/h$), however, we saw no evidence of deviations from linear patterns. Comparison of fit statistics of linear to various non-linear regressions confirmed this observation. Multi-parameter polynomials have been used for predicting maximum heights (Burgess and Dawson 2007) but we excluded them from this comparison because of our inability to interpret such relationships mechanistically. The five new (previously unpublished) datasets all had foliage harvested from the top 10% of short and tall tree crowns that were sunlit, canopy dominants, i.e. short trees were sampled in open or short statured forests, not in the understory of taller forests. These new datasets are (source location and contributor in parentheses): *Pinus teocote* (Mexico, Cornejo Oviedo), *Pinus ponderosa* (Oregon, C. Rose), *Pinus sylvestris* (Scotland, M. Mencuccini), *Artemisia tridentata* (California, W. Oechel), *Pseudotsuga menziesii* (Washington, N. McDowell, B. Bond, J. Janisch, A. Schauer, the $\delta^{13}C$ component of this dataset was published by Bond et al. 2008), and the case study *Nothofagus solandrii* (New Zealand, M. Ryan and D. Whitehead). The samples were analyzed on an isotope ratio mass spectrometer (Delta Plus, Finnigan, Bremen, Germany) interfaced with an elemental analyzer (ESC 4010, Costech, Valencia, CA) located at the Integrated Stable Isotope Research Facility at the Western Ecology Division of the US Environmental Protection Agency, Corvallis, Oregon. Similar to the New Zealand analyses, nitrous oxide was removed by gas chromatography, corrections for ^{17}O were made, and results are presented on the *VPDB* scale.

For published datasets, where possible, we partitioned the data collected in sun-exposed locations from data collected along light gradients within the forest canopy. When possible we also collected ancillary data associated with foliar, environmental or climatic characteristics. A list of the datasets used in this analysis is provided in Table 10.1.

$\delta^{13}C$ data were converted to Δ (Farquhar et al. 1982):

$$\Delta \approx \frac{\delta^{13}C - \delta^{13}C_a}{1 + \delta^{13}C / 1000} \tag{10.4}$$

All $\delta^{13}C$ results were expressed relative to *VPDB*. We obtained annual atmospheric stable carbon isotope ratios ($\delta^{13}C_a$) from the Institute for Arctic and Alpine Research at the University of Colorado and the National Oceanic and Atmospheric Administration, Earth System Research Laboratory. Calculating Δ using Eq. 10.4 allows physiological interpretation of $\delta^{13}C$ by removing the impact of temporally-changing $\delta^{13}C_a$ due to fossil fuel emissions of CO_2 depleted in $\delta^{13}C$ (Leavitt and Long 1988; Keeling et al. 1989). This correction is necessary because a change in the $\delta^{13}C$ of CO_2 used as the substrate for photosynthesis causes a physiologically independent change in the $\delta^{13}C$ of plant material, and because the literature review includes data from >40 year period. Additional sources of analytical error arise from variation in chemical composition of tissues, cellulose extraction and elevation. Lipid, lignin, and cellulose vary in their $\delta^{13}C$ composition and their content within foliage and wood may vary across species and with height. The $\delta^{13}C$ offset for cellulose to whole-tissue ranges from <0.9‰ to >2.5‰ (Schleser 1990; Leavitt and Long 1991; Macfarlane et al. 1999; Loader et al. 2003; Harlow et al. 2006) due in part to variation with species and extraction methods. Only four of our compiled studies (12%) provided cellulose alone, three of which provided only wood cellulose (Grulke and Retzlaff 2001; Monserud and Marshall 2001; Delzon et al. 2004), and one of which provided only foliage cellulose (Phillips et al. 2003). The elevation effect was described above in the *Nothofagus* case study methods section. This effect was difficult to address across the literature review because only 24% of the studies we compiled provided site elevation. The impact may be relatively small; the approximate $\delta^{13}C$ error from assuming constant elevation is ~0.5‰, derived from the standard deviation of 513 m for studies that provided elevation. We highlighted only results in which we were confident the impacts of cellulose extraction and elevation were negligible. In addition, though we choose to analyze species and site specific slopes of Δ versus h for theoretical reasons, there is methodological value as well in that this slope is not affected by the $\delta^{13}C$ variation due to these errors because any error is constant *within* the datasets used to generate the slope.

3 Results

3.1 Case Study

Ψ_l declined more rapidly in the morning in the 11-m *Nothofagus* trees than the 4 m trees (Fig. 10.2a). The average Ψ_l at vapor pressure deficits (D) < 0.8 kPa was −0.83 MPa (se 0.21) and −1.29 MPa (se 0.18) for the 4- and 11-m trees, respectively (unequal variance *t*-test $p = 0.059$). Ψ_l was similar for 4 and 11-m trees at $D > 0.8$ kPa (−1.87 and −1.93 MPa, respectively, $p = 0.18$). For the same sample period, g_s was similar across tree sizes at $D < 0.8$ kPa ($p = 0.31$), but g_s was higher for the 4-m trees at $D > 0.8$ kPa (121.0 vs 91.5 mmol m^{-2} s^{-1} for 4 and 11-m trees, respectively, $p < 0.001$, Fig. 10.2b). K_l followed the same pattern as g_s, with non-significant differences during the morning at $D < 0.8$ kPa ($p = 0.29$) and significantly higher values for the 4-m trees than the 11-m trees at $D > 0.8$ kPa ($p < 0.001$, data not shown). Photosynthesis differed between 4 and 11-m trees (Fig. 10.2c, $p < 0.001$). Leaf [N] was significantly higher in the 4-m trees than the 11-m trees (1.54% and 1.19%, respectively, $p < 0.001$). Leaf $\delta^{13}C$ for the 4- and 11-m trees at this site averaged −25.8 and −24.3 ‰, respectively, equivalent to Δ of 18.3‰ and 16.8‰ ($p < 0.001$, Table 10.1). Wood $\delta^{13}C$ for the 4- and 11-m trees at this site averaged −25.7 and −24.4‰,

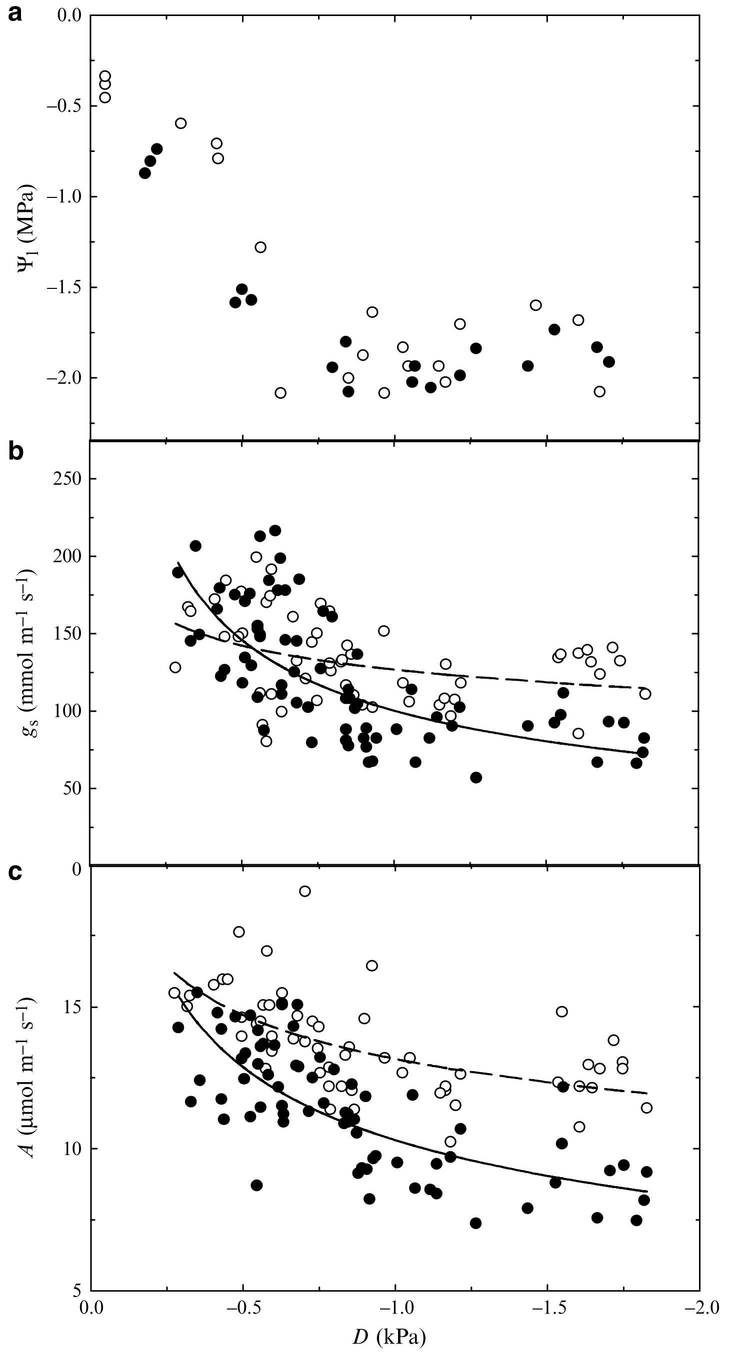

Fig. 10.2 The relationship of D to (**a**) Ψ_l, (**b**) g_s and (**c**) A for 4- (*open circles*) and 11-m (*closed circles*) tall *Nothofagus solandri* trees in New Zealand. The relationships in (**b**) are 4 m: $g_s = 126.8 \cdot D^{-0.166}$ ($r^2 = 0.14$); 11 m: $g_s = 100.4 \cdot D^{-0.541}$ ($r^2 = 0.50$). The relationships in (**c**) are 4 m: $A = 13.2 \cdot D^{-0.16}$ ($r^2 = 0.38$); 11 m: $A = 10.2 \cdot D^{-.321}$ ($r^2 = 0.54$)

Table 10.1 Summary of published and unpublished datasets used in analyses of the Δ–tree height relationship

Species	Height (m)	Δ (‰)	N	Slope (Δ/*h*)	Intercept	R^2	P	Citation
All species, foliar[1]	0.05–113.2	13.6–29.9	820	−0.19 (0.06)	23.4	0.66	0.07	This study
All species, wood[1]	1.01–52.8	14.6–27.2	285	−0.043 (0.01)	18.1	0.38	0.14	This study
Gymnosperms, foliar[1]	**0.16–113**	**13.6–24.9**	**390**	**−0.07 (0.008)**	**24.7**	**0.59**	**0.11**	This study
Lagarostrobos franklinii[2]	0.92–17.0	19.9–24.9	35	−0.13	22.8	0.41	<0.001	Francey et al. (1985)
Lagarostrobos franklinii[3]	0.97–17.0	19.9–21.3	13	−0.01	20.7	0.02	0.6	Francey et al. (1985)
Lagarostrobos franklinii[4]	0.95–14.3	22.2–24.9	6	−0.07	22.6	0.35	0.045	Francey et al. (1985)
Larix occidentalis Nutt[a]	3.85–5.68	19.0–21.4	5	−0.88	24.4	0.56	0.15	Zhang et al. (1994)
Picea rubens/mariana hybrid[a]	0.16–6.47	19.1–23.0	40	−0.48	22.4	0.94	<0.001	Major et al. (2007)
Picea sitchensis[a]	0.63–7.40	19.8–23.6	20	−0.38	22.4	0.42	0.002	Heaton and Crossley (1995)
Pinus elliottii/caribaea hybrid[a]	8.5–13.3	18.7–21.4	40	−0.39	24.6	0.44	<0.001	Xu et al. (2000)
Pinus pinaster	8.46–28.4	17.6–19.2	8	−0.03	19.2	0.22	0.24	Delzon et al. (2004)
Pinus ponderosa[9]	1.35–30.0	15.4–18.8	14	−0.091	19.4	0.63	<0.001	This study
Pinus ponderosa	2.10–37.9	15.5–20.5	27	−0.055	20.3	0.47	0.01	Yoder et al. (1994)
Pinus ponderosa Laws.[a]	0.41–6.83	16.3–18.0	8	−0.09	17.4	0.23	0.23	Grulke and Retzlaff (2001)
Pinus ponderosa[5]	5.60–37.7	18.0–19.7	4	−0.05	19.6	0.97	0.015	Sala and Hoch (2009)
Pinus ponderosa[6]	6.30–34.5	18.2–18.8	4	−0.02	18.9	0.76	0.13	Sala and Hoch (2009)
Pinus sylvestris[9]	0.90–25.0	18.8–21.3	7	−0.027	21.3	0.67	0.025	This study
Pinus sylvestris L.[7]	4.88–21.6	21.3–24.4	8	−0.11	24.1	0.49	0.055	Martínez-Vilalta et al. (2007a)
Pinus sylvestris L.[8]	4.08–21.4	20.2–24.4	23	−0.12	23.7	0.35	0.003	Martínez-Vilalta et al. (2007a)
Pinus teocote[9]	6.00–19.0	16.8–19.1	7	−0.001	18.0	0	0.99	This study
Pseudotstuga menzeseii	2.50–56.1	15.7–18.9	13	−0.03	18.5	0.43	<0.001	This study
Pseudotstuga menzeseii	24.0–53.0	16.0–18.1	2	−0.07	19.8	1	N/A	Winner et al. (2004)
Pseudotstuga menzeseii[9]	15.0–55.9	15.7–18.6	3	−0.071	19.7	0.99	0.033	McDowell et al. (2002a)
Sequoia sempervirens	28.7–112	14.8–19.4	15	−0.033	19.9	0.66	<0.001	Ambrose et al. (2009)
Sequoia sempervirens[2]	14.4–66.8	16.1–22.8	38	−0.092	24.1	0.68	<0.001	Burgess and Dawson (2007)
Sequoia sempervirens[2]	44.8–113	13.6–22.8	59	−0.11	28.0	0.71	<0.001	Koch et al. (2004)
Sequoia sempervirens[3]	14.4–53.8	16.7–22.3	15	−0.12	24.6	0.82	<0.001	Burgess and Dawson (2007)

(continued)

Table 10.1 (continued)

Species	Height (m)	Δ (‰)	N	Slope (Δ/*h*)	Intercept	R^2	P	Citation
Sequoia sempervirens[3]	45.0–100	16.5–23.4	11	−0.09	27.1	0.83	<0.001	Ishii et al. (2008)
Sequoia sempervirens[4]	16.5–66.8	16.1–22.8	11	−0.097	24.7	0.78	<0.001	Burgess and Dawson (2007)
Sequoia sempervirens[4]	40.0–80.0	18.6–24.1	31	−0.08	26.7	0.43	<0.001	Ishii et al. (2008)
Sequoia sempervirens[9]	85.5–112	14.4–19.2	17	−0.087	24.8	0.35	0.017	Koch et al. (2004)
Sequoiadendron giganteum	31.8–90.0	14.1–18.2	15	−0.041	19.1	0.66	<0.001	Ambrose et al. (2009)
Thuja plicata	24.0–53.0	13.6–18.2	2	−0.16	22.0	1	N/A	Winner et al. (2004)
Tsuga heterophila	24.0–53.0	16.2–20.0	2	−0.131	23.1	1	N/A	Winner et al. (2004)
Angiosperms, foliar[1]	**0.05–62.95**	**14.8–29.9**	**430**	**−0.33 (0.12)**	**22.1**	**0.76**	**0.026**	This study
Temperate[1]	**0.05–62.95**	**14.8–25.8**	**129**	**−0.56 (0.30)**	**23.2**	**0.76**	**0.06**	This study
Tropical[1]	**0.15–42.9**	**17.2–29.9**	**350**	**−0.18 (0.03)**	**23.0**	**0.74**	**0.01**	This study
Acer grandidentatum[a]	4.50–6.00	18.2–22.9	6	−2.4	33.1	0.91	0.004	Buchmann et al. (1997a)
All (*Alnus, Fraxinums, Ulmus*)	0.00–20.0	18.2–26.4	79	−0.2	23.6	0.53	<0.001	Hanba et al. (1997)
Alnus hirsute Turcz.	0.92–19.9	19.9–23.6	2	−0.19	23.8	1	N/A	Hanba et al. (1997)
Amazon Ji-Parana	0.72–32.9	19.8–27.2	10	−0.14	26.7	0.56	0.012	Ometto et al. (2002)
Amazon Manaus	0.33–31.8	22.0–29.9	7	−0.25	29.1	0.87	0.002	Ometto et al. (2002)
Amazon Saantarém	0.33–26.9	21.9–28.9	8	−0.25	29.5	0.92	<0.001	Ometto et al. (2002)
Amazon spp.	2.57–52.8	17.9–29.0	204	−0.066	26.1	0.1	<0.001	Martinelli et al. (1998)
Artemisia tridentate[9]	0.50–1.50	14.8–18.0	9	−0.81	17.3	0.16	0.29	This study
Castanopsis chinensis	2.95–23.9	21.2–23.4	3	−0.1	23.7	0.99	0.021	Ehleringer et al. (1986)
Chrysothamnus nauseosus	0.05–1.65	18.1–23.4	49	−2.57	22.3	0.74	<0.001	Donovan and Ehleringer (1994)
Cryptocarya chinensis	2.00–20.0	24.7–27.3	2	−0.24	27.5	1	N/A	Ehleringer et al. (1986)
Eucalyptus diversicolor	13.8–63.0	18.8–23.0	36	−0.064	23.7	0.56	<0.001	Burgess and Dawson (2007)
Eucalyptus saligna[10a]	1.43–7.90	21.1–23.4	23	−0.22	23.3	0.52	<0.001	Barnard and Ryan (2003)
Eucalyptus saligna[11a]	5.43–26.3	22.5–26.2	34	−0.18	27.5	0.76	<0.001	Barnard and Ryan (2003)
Fagus sylvatica L.	1.97–26.8	17.4–23.3	8	−0.12	23.7	0.98	<0.001	Schleser (1992)
Fraxinus mandshurica Rupr.	0.16–19.9	19.3–25.3	16	−0.27	24.2	0.9	<0.001	Hanba et al. (1997)
Juglans regia L.[a]	0.50–4.98	18.4–22.0	10	−0.76	22.7	0.91	<0.001	Le Roux et al. (2001)

Machilus velutina	1.00–14.9	21.3–27.1	2	–0.41	27.5	1	N/A	Ehleringer et al. (1986)
Nothofagus solandri[9]	4.00–11.0	16.8–19.1	2	–0.22	19.2	1	N/A	This study
Parashorea chinensis	35.0–49.9	20.1–21.6	4	–0.099	25.1	0.96	0.019	He et al. (2008)
Populus tremuloides[a]	2.00–6.00	17.7–20.4	6	–0.38	20.6	0.51	0.11	Buchmann et al. (1997a)
Quercus garryana[9]	10.0–25.0	15.6–16.9	2	–0.07	18.1	1	N/A	Phillips et al. (2003)
Schima superba	1.89–23.9	21.6–24.7	4	–0.13	24.9	0.94	0.03	Ehleringer et al. (1986)
Tropical[3]	0.15–25.0	17.2–25.4	26	–0.18	22.2	0.51	<0.001	Broadmeadow et al. (1992)
Tropical[4]	0.15–30.0	19.0–29.2	23	–0.11	24.8	0.25	0.015	Broadmeadow et al. (1992)
Ulmus davidiana Planch.	0.20–20.0	19.1–25.8	13	–0.28	24.0	0.69	< 0.001	Hanba et al. (1997)
Gymnosperms, wood[1]	**1.01–37.9**	**14.6–20.5**	**265**	**–0.029 (0.01)**	**16.8**	**0.31**	**0.16**	This study
Pinus monticola	1.01–34.5	14.9–16.4	77	–0.014	15.8	0.18	<0.001	Monserud and Marshall (2001)
Pinus ponderosa	1.14–32.5	14.6–16.8	80	–0.039	16.4	0.66	<0.001	Monserud and Marshall (2001)
Pinus ponderosa	1.35–30.0	15.4–18.8	12	–0.03	16.7	0.21	0.14	This study
Pinus ponderosa	2.10–37.9	15.5–20.5	12	–0.06	19.0	0.49	0.005	Yoder et al. (1994)
Pseudotstuga menzeseii	2.69–28.9	15.4–17.0	84	–0.002	16.1	0	0.68	Monserud and Marshall (2001)
Angiosperms, wood[1]	**1.97–52.8**	**16.8–29.0**	**81**	**–0.067 (0.03)**	**20.2**	**0.49**	**0.07**	This study
Amazon	2.57–52.8	17.9–29.0	71	–0.070	22.8	0.14	0.004	Martinelli et al. (1998)
Fagus sylvatica L.	1.97–26.8	17.4–23.3	8	–0.020	18.5	0.33	0.14	Schleser (1992)
Nothofagus solandri	4.00–11.0	16.8–19.1	2	–0.110	19.4	1.00	N/A	This study

Values include range of tree heights (m), range of Δ (‰), sample size (n), slopes (‰ m^{-1}) and regression statistics. Data are grouped by tissue type (foliage, wood), and vegetation type (gymnosperm and angiosperm), with averages (and total n) provided in the first row for each group (*standard errors in parentheses*). The averages include only datasets in which the trees approached the maximum potential height for that species at that site. Samples were collected within individual trees at different heights unless indicated otherwise.

Key: 1: average for the group, 2: sunny and shaded samples combined, 3: sunny, 4: shaded, 5: moist, 6: dry, 7: site 2, 8: sites 1 and 3 combined, 9: tree tops, 10: young, 11: old

[a] Trees sampled did not approach maximum potential height of that species at that site

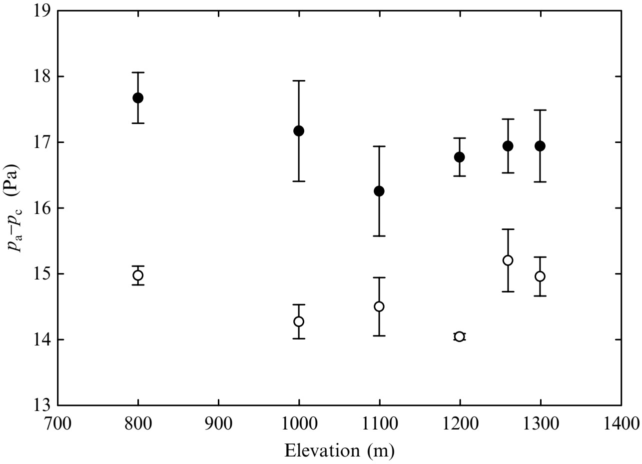

Fig. 10.3 The partial pressure difference between chloroplast and atmospheric CO_2 ($p_a - p_c$) calculated from foliar $\delta^{13}C$, across the *Nothofagus solandri* elevation transect in New Zealand. *Open circles* are short trees and *closed circles* are tall trees. *Bars* are standard errors

respectively, equivalent to Δ of 19.0 and 18.3‰ (p = 0.06, Table 10.1). For the elevation transect, leaf [N] was significantly higher for the short trees compared to the tall trees (1.27% and 1.04%, respectively, p = 0.002). $p_a - p_c$ calculated from foliage $\delta^{13}C$ averaged 14.7 and 17.0 Pa for the short and tall trees, respectively ($p < 0.001$, see Fig. 10.3). There was no trend in the $p_a - p_c$ difference between height classes with elevation (p = 0.22).

3.2 Global Patterns

We found 31 published datasets for inclusion with our five new datasets. This included a total of 15 gymnosperm and 23 angiosperm species, although we note that three publications from the Amazon sampled across a large numbers of species (Broadmeadow et al. 1992; Martinelli et al. 1998; Ometto et al. 2002), which we combined for analyses. After separation of all the individual datasets within publications (i.e. by species or sunny vs shady), we had a total of 61 regressions. These included 13, 48 and 0 from tropical, temperate and boreal regions, respectively. All gymnosperm datasets were from the temperate zone, whereas the angiosperm datasets were evenly divided between temperate and tropical zones. There was a total of 59 datasets of foliage $\delta^{13}C$, 9 of wood $\delta^{13}C$, and five studies that included both. The datasets spanned a range of maximum heights of 1.5–113 m and a Δ range of 13.6–29.9‰ (equivalent to $\delta^{13}C$ of −21.4 to −36.8‰, Table 10.1, Fig. 10.4a). Mean annual precipitation, for the 16 studies that provided precipitation data, ranged from 374 to 4,000 mm.

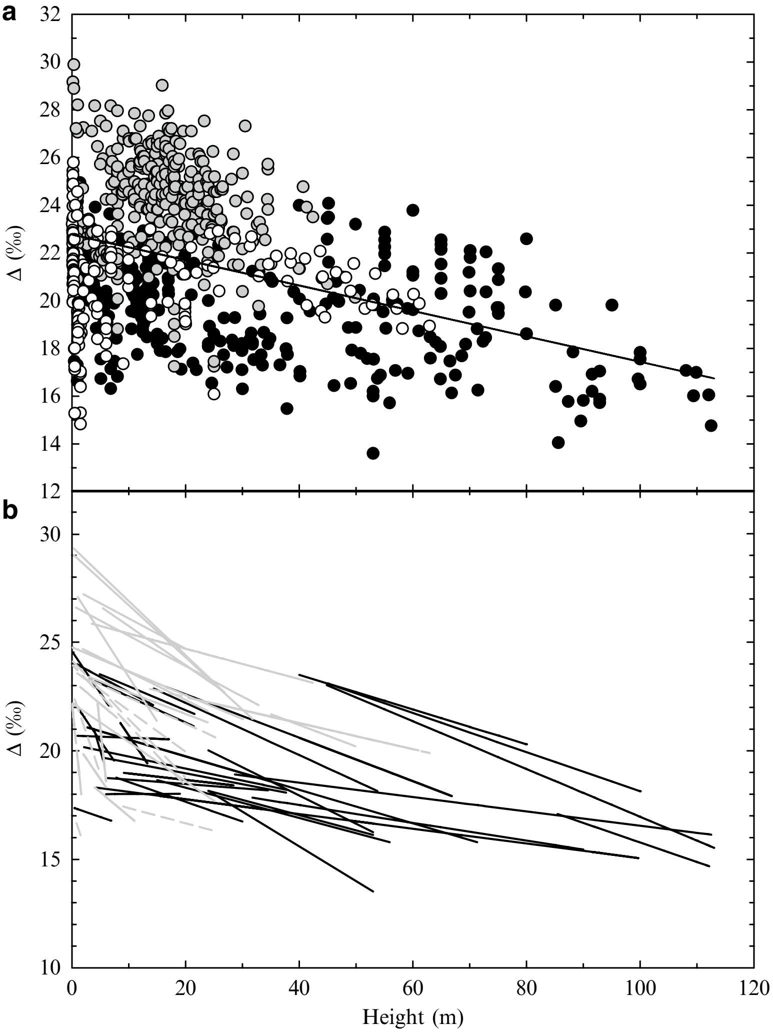

Fig. 10.4 (**a**) The relationship between Δ calculated from foliar $\delta^{13}C$ and height above the ground for temperate gymnosperms (*black circles*) and angiosperms (*open circles*), and tropical angiosperms (*gray circles*). Data include samples collected at different heights within trees as well as at the tops of individual trees of different heights. The relationship for all foliar datasets combined was: $\Delta = -0.053 \bullet \text{height} + 22.77$ ($r^2 = 0.25$, $p < 0.001$). (**b**) Individual regressions for each of the 59 datasets. Gymnosperms, temperate angiosperms, and tropical angiosperms are represented by *solid black*, *dashed gray*, and *solid gray lines*, respectively

Δ declined with increasing height for all foliar datasets (a negative Δ/h, Table 10.1) with 83% significant at $P < 0.10$. The consistent linear declines can be seen graphically in Fig. 10.4b, in which the regression line for each data set from Table 10.1 is shown, with the different lines denoting tropical angiosperms, temperate angiosperms,

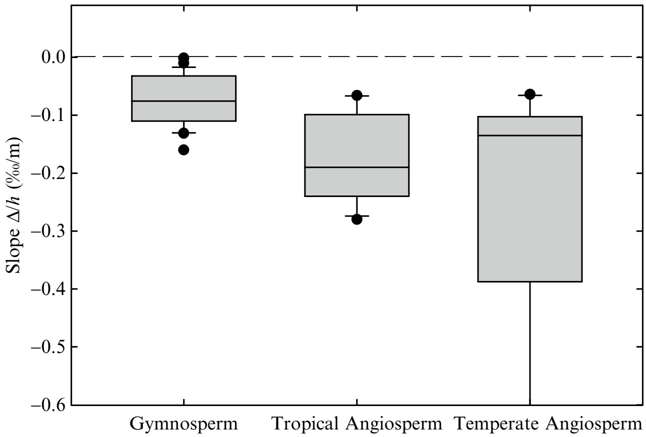

Fig. 10.5 Box plots summarizing the slopes of Δ to *h* for each dataset within gymnosperms and angiosperms (tropical and temperate). Box plots show the lower quartile, the median, and the upper quartile (*the box*), the upper and lower ten percentile values (*the thin lines*, and the range of the observations (*the closed circles*). Note the scale was held to a slope of −0.6‰ m^{-1} for clarity, which omits only the *Chrysothamnus* slope of −2.57‰ m^{-1}. All observations had a negative slope

and temperate gymnosperms. For all species that approached their maximum heights, the mean slope of Δ with *h* was −0.19‰ m^{-1}. Tropical angiosperms had higher Δ than either temperate angiosperms or gymnosperms (4, Table 10.1). The mean slope was shallowest for gymnosperms (−0.07‰ m^{-1}), steepest for temperate angiosperms (−0.56‰ m^{-1}), and intermediate for tropical angiosperms (−0.18‰ m^{-1}, Fig. 10.5). The mean values are heavily influenced by outliers, particularly for temperate angiosperms (e.g., the arid shrub *Chrysothamnus* had a slope of −2.57 ‰ m^{-1}). The median values for these three groups were −0.08, −0.24, and −0.20‰ m^{-1}, respectively (Fig. 10.5). The single foliar dataset which did not exhibit a negative slope was from *Eucalyptus saligna* trees in which the maximum height included in the dataset was only 40% of the site- and species-specific maximum (D. Binkley 2010). The within-canopy declines in Δ with increasing *h* in this dataset were consistent with expectations, but in contrast to the global trend, canopy-top Δ was higher at the tops of tall trees than small trees. It is important to note that studies in which the trees did not approach their maximum height had relatively high slopes (mean −0.59‰ m^{-1}) and were thus excluded from averages calculated across biomes, vegetation type, tissue type, etc. (Table 10.1, Zhang et al. 1994; Heaton and Crossley 1995; Buchmann et al. 1997a; Xu et al. 2000; Le Roux et al. 2001; Grulke and Retzlaff 2001; Barnard and Ryan 2003; Major et al. 2007).

Δ declined with increasing height for all wood datasets (Table 10.1, Fig. 10.6), with 50% of those studies significant at $P < 0.10$. The slope of Δ with increasing *h* was shallower than for foliage (Table 10.1). Similar to the foliage data, the wood slope was steeper and Δ was higher for angiosperms than gymnosperms (Table 10.1). Wood calculated Δ was lower than foliar Δ, as indicated by the lower intercepts (Table 10.1, Fig. 10.6).

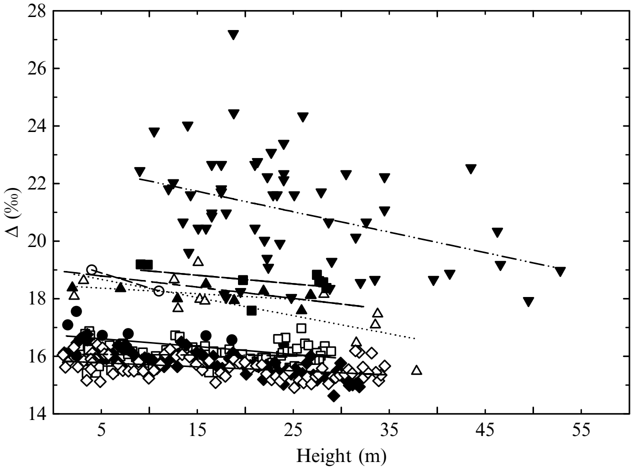

Fig. 10.6 The relationship between stemwood Δ and height for the nine stemwood datasets in this study, including extracted cellulose and whole-tissue data. The data include *Pinus ponderosa* (C. Rose, 2010 – *filled circles*, Yoder et al. 1994 – *upward open triangles*, and Monserud and Marshall 2001 – *filled diamonds*), *Nothofagus* (this study – *open circles*), Amazonian species (Martinelli et al. 1998 – *downward filled triangles*), *Pinus pinaster* (Delzon et al. 2004 – *filled squares*), *Fagus sylvatica* (Schleser 1992 – *upward filled triangles*), and *Pseudotsgua menziesii* (*open squares*) and *Pinus monticola* (*open diamonds*) from Monserud and Marshall (2001)

In five publications the authors sampled both sunlit and shaded crowns of trees. Additionally, sunlit and shaded crowns were sampled at the same *Pseudotsuga menziesii* sites by different groups. These datasets allowed us to test the hypothesis that the Δ response to *h* is exacerbated by light. The compiled sunlit and shaded data are shown in Fig. 10.7. The sunlit and shaded regression lines were offset from each other, with a steeper slope for the shaded than the sunlit trees (–0.065 vs –0.050‰ m^{-1}, respectively) and the shaded intercept more positive than the sunlit intercept (24.0 vs 24.2‰, respectively). To examine the consistency of the sunlit versus shaded Δ/*h* relationship within species, we plotted the sunlit and shaded *Sequoia sempervirens* data from three different publications (Fig. 10.8). Each study yielded results generally similar to the overall comparison, with a clear offset between the shaded and sunlit trees such that Δ was higher for any given *h* for shaded trees compared with sunlit trees.

Studies in which plants had maximum heights less than 20 m tended to have slopes steeper than –0.2‰ m^{-1}, however, most of the tall trees in this range were not near their maximum height (or local maximum height was not quantified), so interpretation of this result is ambiguous. There was also no relationship between the Δ/*h* slope and mean annual precipitation for angiosperms or gymnosperms (data not shown). There was, however, a negative relationship between minimum Δ (canopy top) and maximum height across all datasets (Fig. 10.9). We examined the relationship of Δ and Δ/*h* to structural and nutrient parameters (e.g. Eq. 10.3), however, no clear patterns emerged due in part to the limited availability of these ancillary measurements in the literature.

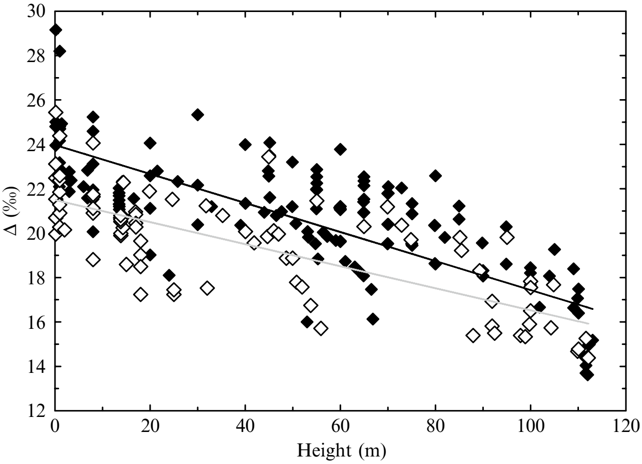

Fig. 10.7 The relationship between Δ calculated from foliage tissue and height for sunlit (*open diamonds*) and paired shaded (*closed diamonds*) trees. Data sets included are *Sequoia sempervirens* (Koch et al. 2004; Burgess and Dawson 2007; Ishii et al. 2008), Amazonian species (Broadmeadow et al. 1992), *Lagarostrobos franklinii* (Francey et al. 1985), and *Pseudotsuga menziesii* (McDowell et al. 2002a; Winner et al. 2004, this study). The regression lines are sunlit: Δ = −0.050 • height + 21.5, $r^2 = 0.58$, p = <0.001 (*dark line*), and shaded: Δ = −0.065 • height + 24.0, $r^2 = 0.64$, p = <0.001 (*gray line*)

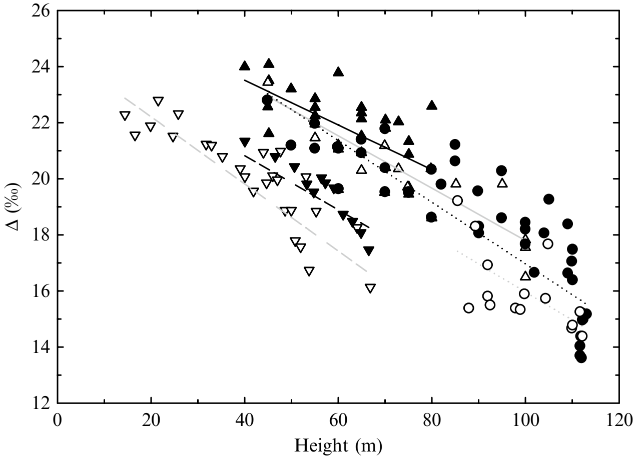

Fig. 10.8 The relationship between Δ (foliar) and height for sunlit and shaded samples for three *Sequoia sempervirens* studies. Shaded samples (*filled symbols*) were collected from trees in relatively closed canopies in contrast to sunlit samples (*open symbols*), which the authors indicated were collected from sunny or otherwise exposed locations. The regressions are: Koch et al. (2004, *circles*) shaded Δ = −0.11 • height (m) + 28.0, $r^2 = 0.71$, p = <0.001, sunlit Δ −0.10 · height (m) + 26.0, $r^2 = 0.46$, p = 0.017, Ishii et al. (2008, *up triangles*) shaded Δ = −0.08 • height (m) + 26.7, $r^2 = 0.43$, p = <0.001, sunlit Δ = −0.09 · height (m) + 27.1, $r^2 = 0.84$, p = <0.001, Burgess and Dawson (2007, *down triangles*) shaded Δ = −0.10 · height (m) + 24.7, $r^2 = 0.78$, p = <0.001, sunlit Δ = −0.12 · height (m) + 24.6, $r^2 = 0.82$, p = <0.001

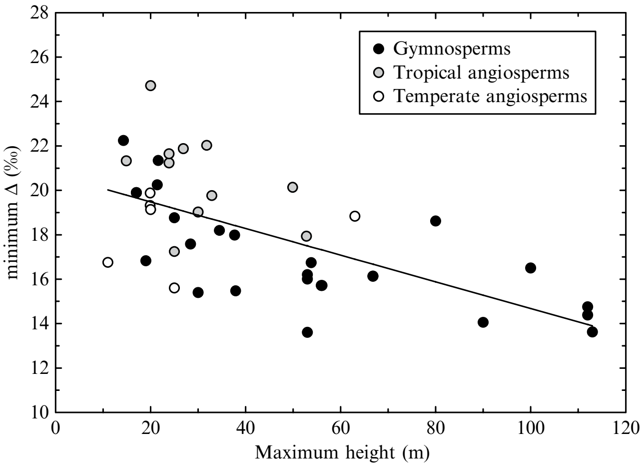

Fig. 10.9 The relationship between minimum Δ (canopy top) and maximum height. Shrubs (*Chrysothamnus* and *Artemesia*) and trees that did not approach their maximum heights were excluded. The regression line is for all data: minimum Δ = –0.06 · height + 20.7, $r^2 = 0.41$, p = <0.001

4 Discussion

Δ declined with increasing height in all 37 datasets and 61 regressions (Fig. 10.4). This decline results from multiple factors that change with increasing height such as increasing light availability and atmospheric $\delta^{13}C$, and decreasing water potential and hydraulic conductance. These changes drive concomitant changes in leaf mass per area, g_i, g_s, and leaf nutrient content. Despite this complexity, the constant decline in Δ with *h* found in our broad review demonstrates the existence of a consistent global relationship. The detailed case study results from *Nothofagus* demonstrate the combined importance of K_l, g_s and *A* on the dependence of Δ upon *h* (Fig. 10.2). We devote the discussion to examination of the driving mechanisms and how they are manifest in our observations.

4.1 The Response of Leaf-Level Gas Exchange and Δ to h in Nothofagus

Ψ_l, g_s, K_l and *A* all showed differences between tree size classes indicative of a hydraulic constraint on gas exchange (Fig. 10.2). These results are consistent with observations of other species (e.g. Yoder et al. 1994; Hubbard et al. 1999; Kolb and Stone 2000; McDowell et al. 2005; Martínez-Vilalta et al. 2007a) in support of the hydraulic limitation hypothesis (Ryan and Yoder 1997) that K_l is lower in taller trees, forcing greater stomatal closure and hence reduced *A*. There also appears to be a biochemical impact on *A* reflected in reduced internal conductance to CO_2 (g_i) with increasing height. In the *Nothofagus* dataset, *A* was always lower in taller trees, even when g_s was similar (compare Fig. 10.2b and c at $D < 0.8$ kPa). Because leaf [N] was significantly lower in the taller trees, it is likely that photosynthetic capacity was also lower (Field and Mooney 1986). This should drive Δ in the opposite direction of that observed (see below). Lower *A* at the same g_s for tall versus short trees could also result from reduced g_i. Thus, while hydraulics per se appear to play a direct role in driving diel gas exchange patterns, longer term impacts of hydraulics on g_i or leaf [N] appear to also be critical (see also Le Roux et al. 2001; Woodruff et al. 2004; Lloyd et al. 2009).

Foliar Δ and $p_a - p_c$ results for all seven *Nothofagus* sites showed evidence of lower p_c as *h* increased (Table 10.1, Fig. 10.3). This suggests that, for this species in this region, the dependence of Δ on *h* is regionally consistent despite variation in climate associated with elevation.

4.2 Why Does Δ Decline Linearly with Increasing h?

The clearest observation from this review is the linear relationship of Δ with *h* (Figs. 10.4b and 10.6–10.9). This is not consistent with the non-linear expectation according to Darcy's law (Eq. 10.3), confirming that other factors beyond hydraulics drive the response to height. Unfortunately, there was insufficient ancillary data on leaf nutrients, leaf mass per area, g_i, within-canopy CO_2 recycling, or the ratio of *h* to total hydraulic pathlength to determine if general relationships exist between these factors and height or Δ; a comprehensive study of these factors is needed in the future. Recycling of isotopically depleted canopy CO_2 should strengthen the gradient of Δ with *h*; however, field measurements have shown this effect to be relatively small (Lloyd et al. 1996, 1997; Brooks et al. 1997a, b; Buchmann et al. 1997a, b). Leaf nitrogen concentration per unit leaf area and photosynthetic capacity sometimes increase with height (and light availability) due to decreased leaf mass per area (e.g., Bond et al. 1999; Carswell et al. 2000; Barnard and Ryan 2003; Lloyd et al. 2009), which could further strengthen the observed relationship of Δ to *h*. This has been frequently observed in angiosperms, high leaf area forests, and trees that have not reached their maximum heights. In contrast, studies on particularly tall trees often find that leaf nitrogen per unit mass and photosynthetic capacity do not vary or even decline with *h* (McDowell et al. 2002a; Ambrose et al. 2009; Woodruff et al. 2009, *Nothofagus* data from this study). Internal conductance has been shown to increase with light or height (Le Roux et al. 2001; Warren et al. 2003). In two tall species, however, g_i and g_s declined linearly with increased *h* (Ambrose et al. 2009; Mullin et al. 2009; Woodruff et al. 2009). Patterns of g_i with *h* must be interpreted cautiously in light of the challenges to accurate measurement associated with g_i methodologies (Bickford et al. 2009; Pons et al. 2009). Recent evidence from both temperate conifer and tropical angiosperm forests suggests that light availability is a dominant driver of leaf morphology and physiology in the lower canopy while hydrostatic water potential gradients drive variation in the upper canopy (Ishii et al. 2007, 2008; Cavaleri et al. 2010; Ishii 2011).

We propose that the linear relationship between Δ and *h* observed in all 61 regressions results from a combination of factors, but is driven ultimately by the linear dependency of maximum leaf water potential on *h* (–0.01 MPa m^{-1}, Bauerle et al. 1999; Koch et al. 2004). This relationship sets boundaries on physiological properties that impact Δ. First, it sets an upper limit on foliar water potential during expansion, causing increasing leaf mass per unit area with increasing *h* (Marshall and Monserud 2003; Woodruff et al. 2004; Koch et al. 2004; Cavaleri et al. 2010), which may subsequently influence g_i and p_c via shifts in mesophyll surface area (Terashima et al. 2005; Oldham 2008). Second, as maximum xylem water potential declines with increasing *h*, the potential range of xylem water potential must also decline (unless the trees are anisohydric with *h*, which is rarely observed, allows only a few tenths MPa shift, and has consequences for xylem conductance and leaf area, Yoder et al. 1994; McDowell et al. 2002a). For example, if minimum g_s in both 10 and 100 m tall *Sequoia* trees occurred at leaf water potential of −2 MPa, then for the 10 m tall trees there is a Ψ range of 1.9 MPa over which water loss may occur prior to stomatal closure, whereas the Ψ range for the 100 m tree is only 1.0 MPa. This impacts Δ because taller trees spend more time with low g_s and hence low p_c than short trees. This was first demonstrated by Yoder et al. (1994) wherein tall ponderosa pines had the same maximum and minimum photosynthetic rates as neighboring short trees, but closed their stomata hours before the short trees because their minimum water potential was achieved earlier.

If the gravitational dependence of water potential on *h* drives the ultimate linearity of Δ with *h*, then how do the other variables in Eq. 10.3, plus light, nitrogen, and g_i, influence the relationship? At least four factors should enhance the non-linear relationship of Δ with increasing *h*: (1) hydraulic conductance declines non-linearly with *h* (Eq. 10.3, Mencuccini and Grace 1996a; McDowell et al. 2002a), which may be exacerbated by a non-linear increase in pathlength with increasing *h* (Magnani et al. 2000); (2) leaf nitrogen sometimes follows a Beer's law pattern with *h* (i.e. Lloyd et al. 2009); (3) occlusion of stomatal pores by cuticular wax may increase with *h* (England and Attiwill 2007); and (4) individual crown leaf area can increase with *h* to maximize whole-plant photosynthetic gain (Schoettle 1994; Buckley and Roberts 2006). In contrast, homeostatic shifts in plant structure, which operate to hold p_c constant within species and sites (Ehleringer 1993; McDowell et al. 2006), should push the Δ versus *h* relationship towards a linear pattern. Such shifts are well documented to occur with increasing *h*, such as changes in leaf area:sapwood area and root area:sapwood area ratios (Magnani et al. 2000; McDowell et al. 2002b; Mencuccini 2003) and sapwood permeability (England and Attiwill 2007). We propose that Δ moves away from the expected 1/*h* pattern at low heights due to *h*-driven homeostatic shifts (McDowell et al. 2002a, b; Mencuccini 2003) and light-driven leaf-photosynthetic shifts (Fig. 10.10). At some point, however, further shifts become infeasible and subsequent height growth forces Δ back towards the theoretical line from Eq. 10.3 (Fig. 10.10). This hypothesis can be tested by thorough

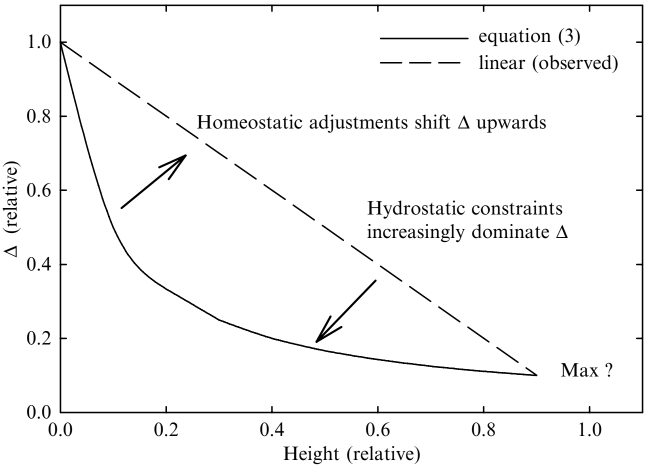

Fig. 10.10 A hypothesis regarding the interactive effects of environmental, physical and homeostatic factors on observed linear dependency of Δ with *h*. Many factors shift in the early phases of height growth to maximize p_c and hence Δ, thereby pushing Δ above the 1/*h* relationship. As height growth continues, the gravitational and hydraulic constraints dominate, forcing Δ to continue to a minimum

accounting of the vertical gradients of the above-mentioned key variables that influence Δ, both within the canopies of tall trees and across the sunlit tops of trees of different heights (e.g. Mullin et al. 2009).

A thorough accounting of all the factors that vary with height and that impact Δ would also aid our understanding of the trend of decreasing minimum Δ with increasing maximum *h* (Fig. 10.9). For the 43 datasets in which trees approached maximum height, there was a 0.06‰ decline in Δ for every meter increase in height. Though it is impossible with this dataset to conclusively interpret this pattern, it does suggest that the minimum Δ and maximum *h* are functionally linked. This may be due to a minimum sustainable p_c that allows a sufficient positive carbon balance at the leaf level. The minimum Δ values shown in Fig. 10.9 correspond to a p_c range of 320–147 ppm. The minimum p_c achievable by C3 plants is thought to be ~100–124 ppm (Tenhunen et al. 1984; Koch et al. 2004; Ward et al. 2005). This minimum Δ appears species- and site-specific (Fig. 10.9), perhaps due to variation in minimum CO_2-compensation points or thresholds for hydraulic failure due to prolonged embolism without refilling (Hacke et al. 2001; McDowell et al. 2002a; Ambrose et al. 2009). Understanding the drivers, consequences and homeostatic limitations of this minimum Δ is an important area for future research.

4.3 Irradiance and Height

In addition to the direct response of Δ to height, irradiance emerged as a clearly detectable environmental effect on Δ in our global review. Δ of sunlit foliage was

0.5‰–3.0‰ lower than that of shaded foliage (Figs. 10.7 and 10.8), consistent with prior observations (Fig. 10.1, Waring and Silvester 1994, also Livingston et al. 1998; Warren and Adams 2000; Le Roux et al. 2001; Geßler et al. 2001; Samuelson et al. 2003; Koch et al. 2004). There was no consistent difference in the Δ–*h* relationship between sunlit and shaded samples (Fig. 10.8). In this analysis, it appears that *h* dominates the trend in Δ while irradiance moderates the absolute values, presumably caused by the increased light interception and photosynthetic capacity with increased height and subsequent reduction in p_c (Ehleringer et al. 1986; Carswell et al. 2000; Lloyd et al. 2009). While *h* is clearly a global driver of Δ, the impact of irradiance on Δ should vary globally as a function of ecosystem leaf area and subsequent light interception profiles (Campbell and Norman 1998; Parker et al. 2002; Koch et al. 2004).

4.4 Patterns with Biomes and Vegetation Type

Clear differences emerged between biomes and vegetation type (gymnosperms and angiosperms). Tropical angiosperms had higher Δ than temperate gymnosperms or angiosperms (Table 10.1, Fig. 10.4). This Δ variation does not correspond with maximum height (data not shown), but does correspond with mean annual precipitation. For the studies that provided mean annual precipitation, it averaged 2,666 mm year^{-1} (n = 6) for tropical angiosperms, compared to 1,518 mm year^{-1} (n = 19) and 1,027 mm year^{-1} (n = 7) for temperate gymnosperms and angiosperms, respectively. Correlations between Δ and precipitation are routinely found in regional or global scale studies (e.g. Schulze et al. 1998; Warren et al. 2001; Bowling et al. 2002) due to the dominant effect of water availability on g_s and p_c. The lack of freezing temperatures in tropical regions may also allow higher g_s and p_c because xylem vessels can grow larger and have subsequently greater hydraulic conductance (Sperry et al. 2006).

The slope of Δ to *h* with biome and vegetation type differed from the absolute Δ values, being smallest for gymnosperms, largest for temperate angiosperms, and intermediate for tropical angiosperms (median values of –0.09, –0.24, and –0.20‰ m^{-1}, respectively, Table 10.1, Fig. 10.5). The greater slope of Δ to *h* indicates greater driving forces for a decline in Δ with *h* and/or greater flexibility of the trees to adjust Δ with height. The latter is consistent with the observation that species with higher sapling photosynthetic rates can achieve greater heights (Thomas and Bazzaz 1999); i.e. trees that start with high *A* may be able to grow relatively taller before *A* reaches threshold minimums. In our review, maximum Δ averaged 25.2‰ for angiosperms compared to 21.0‰ for gymnosperms, and the Δ range (maximum–minimum) was 4.0‰ and 5.8‰, respectively (31% greater for angiosperms). If the theoretical minimum Δ at maximum tree height is a fixed value at 13.6‰ (δ^{13}C of −20.0‰ estimated for *Sequoia sempervirens*, Koch et al. 2004; Burgess and Dawson 2007), then the maximum allowable Δ range is 36% greater for angiosperms than gymnosperms (11.6‰ vs 7.4‰, respectively). This can also be calculated using the minimum Δ observed for angiosperms (17.2‰) and gymnosperms (13.6‰, Fig. 10.9), yielding respective ranges of 7.4‰ and 13.0‰, or 43% greater for angiosperms.

The Δ patterns we observed between and within studies can also be influenced by post-assimilation isotopic effects. For example, differential day versus night respiratory fractionation, differential allocation of day versus night sucrose, and carbon fixation by PEP carboxylase, could all be manifest to influence δ^{13}C of leaf and stem tissues (Cernusak et al. 2009). Our understanding of these post-assimilation effects is rapidly progressing; however, it is premature for us to assess their magnitude without detailed isotopic flux and carbohydrate measurements (e.g. Badeck et al. 2007; Barbour et al. 2007; Brandes et al. 2006; Bickford et al. 2009). Stem tissues are particularly influenced by such post-photosynthetic metabolic effects, e.g. due to mixing of carbohydrate pools during the formation of wood (Helle and Schleser 2004; Ogée et al. 2009; Gessler et al. 2009). We observed a consistent offset between foliage and wood (similar to that summarized by Cernusak et al. 2009) and flatter Δ–*h* relationships in wood than foliage (Figs. 10.4 and 10.6), all consistent with post-photosynthetic effects. By comparing foliage and stem tissues separately we hoped to minimize these effects in comparisons of Δ to *h*. Inter-tree comparisons of different sized trees may be possible using either foliage or wood δ^{13}C, however, we suggest that foliage δ^{13}C data may better integrate gas exchange when comparing Δ to *h* within trees.

4.5 Mixing Apples and Oranges

Five methodological constraints emerged from our global review that would benefit from careful research in the future. First, as noted earlier, foliage provides a better index of Δ in relation to *h* than wood, possibly due to the impacts of post-photosynthetic fractionation and mixing on the δ^{13}C composition of wood. Second, datasets from boreal forests were notably absent. Filling this biome-gap could yield new information since there was a clear pattern between tropical and temperate regions (Figs. 10.4 and 10.5) and since different climate drivers may dominate in boreal regions. Third, we need to separate the impacts of *h* on Δ between tops of differing size trees versus within crowns of tall trees. Comparing sunlit tops of trees of varying sizes excludes the confounding influence of light, allowing one to directly test the impacts of size-related hydraulics on Δ (e.g. McDowell et al. 2002a; Barnard and Ryan 2003; Koch et al. 2004, Figs. 10.7 and 10.8). Measuring within-canopy gradients avoids the assumptions of space-for-time substitution, however, and provides useful information on the combined light/hydraulic impacts on Δ, as well as information on within-tree homeostatic adjustments (Hubbard et al. 2002; Ishii et al. 2008). Since both approaches are useful, combining them in future studies may reveal more information than studying only tree tops or only within-tree gradients (Mullin et al. 2009). Fourth, as noted earlier, comprehensive measurements of environmental and physiological drivers of Δ with *h* are needed within studies, including light, humidity, gravitational potential, hydraulic conductance, gas exchange, leaf mass per area, leaf nutrients, woody anatomy, and leaf area:sapwood area ratios. Fifth, to understand the response of Δ throughout the height continuum, experimental designs should include trees near their site- and species-specific maximum heights. The slope of Δ to *h* tended to be steeper in studies of trees that were not at their maximum heights, suggesting that different responses are manifest during different phases of height growth. This may account for the outlier result from Barnard and Ryan (2003), in which the tallest measured trees had higher Δ rather than the expected lower Δ, but those trees were only 40% of maximum *h* for that site (D. Binkley 2010). Notably, factors such as leaf area:sapwood area follow a hyperbolic shape with increasing values to middle-heights followed by declining values to maximum heights in *Eucalyptus saligna* (N. McDowell 2010), thus Δ may also follow a similar pattern. Regardless, studies of height-related variation in Δ within trees that are not near their maximum heights may yield different insights than studies covering the entire height continuum.

5 Conclusions

Through our global review of 36 datasets with 38 species, we observed consistent, linear declines of Δ with *h*. The most parsimonious explanation of this result is that gravitational constraints on maximum leaf water potential set an ultimate boundary on the shape and sign of the relationship. These hydraulic constraints are manifest both over the long term through impacts on leaf structure, and over diel periods via impacts on K_l, g_s and *A*. Shading induces a positive offset to the linear decline, consistent with light limitations reducing *A* and increasing p_c at a given height (Fig. 10.1, Waring and Silvester 1994). Biome differences between tropical and temperate forests were more important in predicting Δ and its relationship to *h* than wood vasculature type (angiosperm vs gymnosperm). It is not yet clear how g_i varies with leaf mass per area (Terashima et al. 2005), but limited datasets in particularly tall, temperate conifers suggest that photosynthetic capacity does not vary dramatically with *h* when compared between tree-tops, while both g_s and g_i decline in unison with *h* within canopy gradients. We agree with previous conclusions that light is a critical variable low in the canopy whereas hydrostatic constraints dominate the Δ/*h* relationship in the upper canopy. A trend of increasing maximum *h* with decreasing minimum Δ suggests that trees that become particularly tall are adapted to tolerate particularly low values of p_c.

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