Tree and Forest Responses to Interacting Elevated Atmospheric CO$_2$ and Tropospheric O$_3$: A Synthesis of Experimental Evidence

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Dedication: We dedicate this chapter to the memory of our friend and colleague, Dr. Fitzgerald Booker. Fitz made many lasting contributions to air pollution science through his primary research and leadership in organizing informal and formal research collaborations, such as the Air Pollution Workshop and NE-1013. He also contributed to the career advancement of many by unselfishly sharing his lab, expertise and time. He was a meticulous editor and author, careful researcher and patient teacher. His life is a reminder to appreciate each day, be helpful to those around us, and do good work.

9.1 INTRODUCTION

It has long been recognized that development of ecosystem models to project the effects of global change on terrestrial carbon, water and nutrient cycling must consider how multiple environmental factors *interact* to influence ecosystem composition and function (Mooney et al., 1991; Niinemets, 2010). Recent studies have shown explicitly that responses to single environmental stress factors are often (usually) not additive, suggesting that conclusions from single factor experiments be interpreted with caution (Dieleman et al., 2012). Given the limitations of our ability to understand higher-order interactions of more than three or four factors at a time, and the practical limitations of conducting such experiments on large scales, the question is: Which factors should be studied? Because of its long mean-residence time in the atmosphere, continued increase in emissions and direct effects on plant physiological processes, it has been widely concluded that elevated atmospheric CO_2 (eCO_2), and especially how it interacts with rising global temperature, is of particular importance (Calfapietra et al., 2010; Dieleman et al., 2012). Similarly, both nitrogen (N) limitation and enrichment continue to be problems around the world, and how N availability interacts with eCO_2 continues to be an active area of research (Calfapietra et al., 2010; Reich et al., 2006). However, the interaction of eCO_2 and elevated tropospheric O_3 (eO_3) is uniquely compelling in that both pollutants are assimilated via gas exchange of the leaf, directly influence leaf area development and stomatal conductance and alter plant physiology in generally antagonistic ways, with potential to cascade through ecosystem processes (Karnosky et al., 2003).

The transition to a new energy infrastructure with significantly decreased fossil CO_2 emissions is still decades away and there is rapid economic growth but lagging environmental policy in many parts of the world; therefore, the interaction of $eCO_2 \times eO_3$ will continue to impact terrestrial ecosystems over a planning horizon beyond 2100. Although air pollution policy in Europe and North America has largely succeeded in decreasing peak O_3 concentrations in those regions (see Chapter 5), economic modelling studies and documented transoceanic O_3 transport suggest increasing background concentrations worldwide for decades to come (Fowler et al., 1999; Li et al., 2002). Globally, production of eO_3 exceeds its consumption. Regionally, rapid economic development in Central Europe, Asia and South America is adding new sources to the global eO_3 burden (see also Koike et al., Pandey et al., Kozovits and Bustamante, Laasko et al., this

volume). It is possible these new source regions will experience a similar co-evolution of economic development and degradation of air quality, followed by improved scientific understanding and development of enlightened environmental policy, as occurred elsewhere (e.g. the Clean Air Act of the U.S. dates to 1970). Lessons learned from the decades of research on eCO_2 and eO_3 could benefit social development in ways that preserve environmental quality, locally and globally. In particular, development of metrics for eO_3 dose–response relationships is still a work in progress, and widespread adoption of air quality standards would be beneficial.

In order to improve our predictive understanding of terrestrial ecosystem responses to climate change and to protect current environmental quality, there is a pressing need to summarize the available data on interacting eCO_2 and eO_3, identify gaps in knowledge and make recommendations for future research. We sought to accomplish these goals by surveying the peer-reviewed literature with the following questions in mind:

a. Do the available data support the hypothesis of increased leaf-level photosynthesis and decreased stomatal conductance under eCO_2, and the inverse under eO_3?
b. Do the available data support the hypothesis that forest productivity increases under eCO_2 and decreases under eO_3?
c. Do the available data support the hypothesis that litter quality and decomposition rates will be affected by eCO_2 and eO_3, resulting in changes in soil organic carbon (SOC) pools?
d. What is the net effect of the *interaction* of eCO_2 and eO_3 on all of the above and do responses change with tree/forest age or length of exposure?

9.2   LITERATURE SURVEY METHODS

To focus on $eCO_2 \times eO_3$ interaction experiments, we surveyed the peer-reviewed scientific literature from 1990 to 2012 using academic Internet search engines with access to all major databases in the natural sciences (e.g. AGRICOLA, CAB, Plant Science, Ecology Abstracts, BIOSIS, Environmental Science & Pollution Management, JSTOR, Web of Science). We restricted the review to studies that simultaneously applied fumigation of eCO_2 and eO_3 and used only widely accessible primary sources (no proceedings, reviews/meta-analyses, edited book volumes, textbooks, abstracts, etc.). For each variable (listed in Tables 9.1–9.3), we searched the keywords: variable name, 'elevated CO_2', 'carbon dioxide', 'tropospheric O_3', 'ozone', 'forest', 'tree' and 'interaction'. If a paper contained values for multiple species or communities, they were included in the database as individual observations. If other treatments were part of the experiment, we used the values for the control in the experiment; however this occurred only on a few occasions. Trees were grouped as 'young', if the plants were 5 years of age or less,

TABLE 9.1 Effects of Elevated Atmospheric CO_2 (eCO_2) and Elevated Tropospheric O_3 (eO_3) on Selected Physiology and Water Use Parameters for Young (5 Years or Less) and Intermediate (6–12 years) Age Trees and Forest Stands

Parameter	Observations GC:GH:OT: FC	Age (years)	A:E CO_2 exp. (ppm)	A:E O_3 exp. (ppb)	Control (mean, n, CV)	eCO_2 (%, n, CV)	eO_3 (%, n, CV)	e$CO_2 \times$ eO_3 (%, n, CV)	Sources
Young: 5 years or less									
A_{CO_2}	10:0:2:6	1.7 (1.0)	358:605 (8:67)	30:73 (19:18)	10.0, 18, 0.58	22.6, 18, 0.50	−12.5, 18, 0.49	13.0, 18, 0.47	Grams et al. (1999), Kull et al. (1996), Loats and Rebbeck (1999), Noormets (2001), Noormets et al. (2010), Olszyk et al. (2002), Sharma et al. (2003), and Volin et al. (1998)
g_s	10:0:4:3	1.7 (1.8)	359:629 (9:69)	30:77 (23:18)	194.4, 17, 0.58	−26.1, 17, 0.61	−9.6, 17, 0.58	−26.4, 17, 0.60	Gardner et al. (2005), Grams et al. (1999), Kull et al. (1996), Loats and Rebbeck (1999), Noormets (2001), Noormets et al. (2001, 2010), Olszyk et al. (2002), Sharma et al. (2003), Volin and Reich (1996) and Volin et al. (1998)
iWUE	9:0:2:2	1.4 (0.9)	358:618 (9:67)	25:74 (20:18)	0.053, 13, 0.36	83.6, 13, 0.27	2.5, 13, 0.33	65.4, 13, 0.32	Kull et al. (1996), Loats and Rebbeck (1999), Olszyk et al. (2002), Sharma et al. (2003) and Volin et al. (1998)

LAI	0:0:0:3	3.7 (1.2)	353:554 (6:10)	36:53 (NA)	2.1, 3, 0.17	14.9, 3, 0.21	−17.6, 3, 0.14	−11.5, 3, 0.19	Isebrands et al. (2001), Karnosky et al. (2005) and Noormets (2001)
Intermediate: 6–12 years								
A_{CO_2}	0:0:3:12	8.6 (1.4)	362:588 (4:60)	31:65 (16:16)	12.5, 15, 0.13	45.0, 15, 0.15	−14.1, 15, 0.11	35.6, 15, 0.16	Darbah et al. (2010), Kets et al. (2010) and Riikonen et al. (2005)
g_s	0:0:0:2	7.5 (0.7)	360:560 (NA)	20:48 (NA)	300.0, 2, 0.19	−19.2, 2, 0.19	−6.8, 2, 0.11	−24.3, 2, 0.09	Kets et al. (2010)
iWUE	0:0:0:2	7.5 (0.7)	360:560 (NA)	20:48 (NA)	0.044, 2, 0.13	69.1, 2, 0.17	−0.7, 2, 0.17	83.6, 2, 0.09	Kets et al. (2010)
LAI	0:0:0:2	7.5 (0.7)	369:526 (1:1)	35:47 (3:6)	3.9, 2, 0.04	32.4, 2, 0.16	−25.6, 2, 0	6.4, 2, 0.05	Uddling et al. (2008)

No data were available from mature trees. 'Observations' refers to the number of observations from facilities of the following types: GC, growth chamber; GH, green house; OT, open-top chamber; FC, FACE. Age, A:E CO_2 and O_3 exposures consist of the mean for ambient:elevated levels of CO_2 and O_3 and respective standard deviations.

TABLE 9.2 Effects of Elevated Atmospheric CO_2 and Tropospheric O_3 on Selected Biomass and Net Primary Production (NPP) Parameters for Young (5 Years or Less) and Intermediate (6–12 Years) Age Trees and Forest Stands

Parameter	Observations GC:GH:OT: FC	Age (years)	A:E CO_2 exp. (ppm)	A:E O_3 exp. (ppb)	eCO_2 (%, n, CV)	eO_3 (%, n, CV)	$eCO_2 \times eO_3$ (%, n, CV)	Sources
Young: 5 years or less								
Foliage	10:4:12:3	2.9 (2.1)	368:634 (19:89)	27:88 (16:46)	18.4, 26, 1.24	−15.8, 28, 1.07	18.3, 28, 3.92	Broadmeadow and Jackson (2000), Dickson et al. (1998, 2001), Gardner et al. (2005), Gaucher et al. (2003), King et al. (2005), Liu et al. (2004), Loats and Rebbeck (1999), Rebbeck and Scherzer (2002), Richet et al. (2012), Rodenkirchen et al. (2009) and Watanabe et al. (2010)
Stem/wood	11:8:9:3	3.2 (2.2)	374:637 (20:94)	27:84 (16:39)	22.8, 28, 1.05	−10.2, 31, 1.82	10.5, 31, 2.47	Dickson et al. (1998, 2001), Gardner et al. (2005), Gaucher et al. (2003), King et al. (2005), Kozovits et al. (2005), Liu et al. (2004), Loats and Rebbeck (1999), Polle et al. (1993), Rebbeck and Scherzer (2002), Richet et al. (2012), Rodenkirchen et al. (2009) and Watanabe et al. (2010)
Coarse root	5:4:1:3	4.6 (1.4)	376:663 (23:70)	33:86 (9:46)	34.0, 11, 0.77	−2.7, 12, 4.01	23.3, 12, 1.35	King et al. (2005), Liu et al. (2004), Rebbeck and Scherzer (2002), Rodenkirchen et al. (2009) and Watanabe et al. (2010)

Fine root	6:4:1:3	4.5 (1.4)	379:665 (25:68)	33:86 (8:44)	41.8, 11, 0.93	−8.2, 12, 2.16	37.1, 11, 1.2	King et al. (2005), Liu et al. (2004), Phillips et al. (2009), Rebbeck and Scherzer (2002) and Watanabe et al. (2010)
FR turnover	1:0:0:0	3.0 (NA)	420:690 (NA:NA)	36:80 (NA:NA)	26.0, 1, NA	5.0, 1, NA	0.0, 1, NA	Phillips et al. (2009)
Total AG	8:0:5:3	3.4 (1.9)	361:641 (16:73)	34:79 (10:43)	26.8, 16, 0.54	−9.7, 16, 1.28	16.7, 16, 1.27	Broadmeadow and Jackson (2000), Gardner et al. (2005), King et al. (2005), Loats and Rebbeck (1999), Polle et al. (1993), Riikonen et al. (2004) and Utriainen et al. (2000)
Total BG	9:0:11:3	2.5 (1.8)	365:609 (21:85)	27:88 (17:44)	26.5, 21, 0.82	−19.1, 23, 1.10	3.6, 22, 3.87	Broadmeadow and Jackson (2000), Dickson et al. (1998, 2001), Gaucher et al. (2003), King et al. (2005), Loats and Rebbeck (1999), Olszyk et al. (2001), Rodenkirchen et al. (2009) and Utriainen et al. (2000)
Total AGBG	9:0:11:3	2.5 (1.8)	362:608 (14:84)	26:89 (18:44)	29.6, 21, 0.63	−18.3, 23, 1.04	14.5, 23, 2.25	Broadmeadow and Jackson (2000), Dickson et al. (1998, 2001), Gaucher et al. (2003), King et al. (2005), Loats and Rebbeck (1999), Rodenkirchen et al. (2009), Utriainen et al. (2000) and Watanabe et al. (2010)
ANPP	0:0:0:3	3.0 (NA)	348:540 (NA:NA)	37:52 (NA:NA)	40.9, 3, 0.43	−15.9, 3, 0.72	12.1, 3, 0.97	King et al. (2005)

TABLE 9.2 Effects of Elevated Atmospheric CO_2 and Tropospheric O_3 on Selected Biomass and Net Primary Production (NPP) Parameters for Young (5 Years or Less) and Intermediate (6–12 Years) Age Trees and Forest Stands—Cont'd

Parameter	Observations GC:GH:OT: FC	Age (years)	A:E CO_2 exp. (ppm)	A:E O_3 exp. (ppb)	eCO_2 (%, *n*, CV)	eO_3 (%, *n*, CV)	$eCO_2 \times eO_3$ (%, *n*, CV)	Sources
Intermediate: 6–12 years								
Foliage	0:0:4:6	8.7 (2.1)	362:610 (13:94)	46:67 (12:21)	38.0, 10, 0.75	−13.41, 10, 0.61	12.2, 10, 0.75	Kasurinen et al. (2005), King et al. (2005), Riikonen et al. (2004) and Talhelm et al. (2012)
Stem/wood	0:0:2:3	7.2 (1.6)	360:612 (16:98)	46:68 (12:22)	42.9, 5, 0.59	−13.0, 5, 0.81	22.5, 5, 0.68	King et al. (2005) and Riikonen et al. (2004)
Coarse root	0:0:0:3	6.0 (NA)	348:540 (NA:NA)	37:52 (NA:NA)	49.0, 3, 0.38	−19.35, 3, 0.25	13.9, 3, 0.84	King et al. (2005)
Fine root	0:0:0:11	7.4 (0.9)	354:536 (4:3)	36:50 (0.5:0.9)	53.7, 11, 1.65	1.82, 11, 8.08	47.8, 11, 0.72	King et al. (2005), Pregitzer et al. (2008) and Rhea and King (2012)
FR turnover	0:0:0:1	8.0 (NA)	348:540 (NA:NA)	37:52 (NA:NA)	2.8, 1, NA	1.4, 1, NA	17.6, 1, NA	Pregitzer et al. (2008)
Total AG	0:0:2:3	7.2 (1.6)	360:612 (16:99)	46:68 (12:22)	41.3, 5, 0.63	−13.7, 5, 0.83	22.4, 5, 0.73	King et al. (2005) and Riikonen et al. (2004)

Total BG	0:0:2:3	7.2 (1.6)	360:612 (16:99)	46:68 (12:22)	36.8, 5, 0.60	−19.8, 5, 0.57	21.4, 5, 0.92	King et al. (2005) and Riikonen et al. (2004)
Total AGBG	0:0:2:3	7.2 (1.6)	360:612 (16:99)	46:68 (12:22)	40.4, 5, 0.62	−15.0, 5, 0.76	22.1, 5, 0.80	King et al. (2005) and Riikonen et al. (2004)
ANPP	0:0:0:3	6 (NA)	348:540 (NA:NA)	37:52 (NA:NA)	50.8, 3, 0.35	−11.1, 3, 0.97	20.7, 3, 1.12	King et al. (2005)
Total NPP	0:0:0:1	12 (NA)	348:560 (NA:NA)	35:55 (NA:NA)	12.0, 1, NA	8, 1, NA	0, 1, NA	Zak et al. (2011)

No data were available from mature trees. 'Observations' refers to the number of observations from facilities of the following types: GC, growth chamber; GH, green house; OT, open-top chamber; FC, FACE. Age, A:E CO_2 and O_3 exposures consist of the mean for ambient:elevated levels of CO_2 and O_3 and respective standard deviations.

TABLE 9.3 Effects of Elevated Atmospheric CO_2 and Tropospheric O_3 on Selected Litter Biochemical and Decomposition-Related Soil Parameters for Young (5 Years or Less) and Intermediate (6–12 Years) Age Trees and Forest Stands

Parameter	Observations GC:GH:OT: FC	Age (years)	A:E CO_2 exp. (ppm)	A:E O_3 exp. (ppb)	eCO_2 (%, n, CV)	eO_3 (%, n, CV)	$eCO_2 \times eO_3$ (%, n, CV)	Sources
Young: 5 years or less								
Leaf condensed tannins	0:0:0:9	3.8 (0.8)	360:560 (0:0)	41:62 (5:8)	15.5, 9, 1	2.6, 9, 0.6	35.3, 9, 0.9	Holton et al. (2003), Kopper and Lindroth (2003), Parsons et al. (2004, 2008) and Talhelm et al. (2009)
Leaf phenolics	0:0:2:3	2.8 (0.5)	358:600 (4:69)	39:62 (6:8)	8.9, 5, 0.79	−9.9, 5, 0.7	0.5, 5, 1.1	Holton et al. (2003), Kainulainen et al. (2003), Parsons et al. (2004) and Sallas et al. (2001)
Leaf lignin	0:1:0:1	3.5 (2)	360:610 (0:70)	41:63 (7:10)	5.0, 1, NA	−15.4, 2, 0.3	22.5, 2, 1.3	Boerner and Rebbeck (1995) and Parsons et al. (2004)
Leaf C	0:2:0:0	5 (0)	350:750 (0:0)	20:75 (0:0)	−1.0, 2, 1	−1.8, 2, 0.9	−1.9, 2, 1.1	Pfirrmann et al. (1996)
Leaf N	0:3:10:7	3.2 (1.2)	364:657 (9:77)	29:57 (9:12)	−14.2, 16, 0.7	−11.5, 20, 1.1	−27.6, 20, 0.46	Boerner and Rebbeck (1995), Broadmeadow and Jackson (2000), Holton et al. (2003), Kopper and Lindroth (2003), Olszyk et al. (2001), Parsons et al. (2004, 2008), Pfirrmann et al. (1996) and Scherzer et al. (1998)
Leaf C/N	0:0:0:2	3.0 (0)	360:560 (0:0)	45:70 (0:0)	14.9, 2, 0.5	−5.4, 2, 0.7	32.3, 2, 0.6	Lindroth et al. (2001)

Fine root N	0:2:2:0	3.5 (1.7)	355:695 (6:64)	28:70 (9:6)	−2.6, 4, 0.5	4.6, 4, 0.5	−1.6, 4, 1.0	Olszyk et al. (2001) and Pfirrmann et al. (1996)
Litter decomposition (MRT)	0:1:0:5	1.2 (0.4)	360:576 (0:41)	36:58 (0:7)	2.9, 6, 0.9	−2.9, 6, 0.7	47.1, 6, 1.1	Boerner and Rebbeck (1995) and Parsons et al. (2004, 2008)
Soil carbon	0:0:0:1	4 (0)	360:560 (0:0)	46:70 (0:0)	−2.8, 1, NA	5.5, 1, NA	−5.0, 1, NA	Loya et al. (2003)
Intermediate: 6–12 years								
Leaf condensed tannins	0:0:5:10	8.9 (1.6)	363:603 (11:72)	38:58 (6:14)	19.6, 15, 0.7	34.1, 15, 1	46.1, 15, 1.0	Agrell et al. (2005), Couture et al. (2012), Hillstrom et al. (2010), Kasurinen et al. (2007), Liu et al. (2005, 2009) and Peltonen et al. (2005)
Leaf phenolics	0:0:6:4	9.5 (1.6)	360:633 (8:76)	34:53 (6:13)	14.6, 9, 0.6	26.3, 9, 0.9	42.0, 9, 0.9	Couture et al. (2012), Kasurinen et al. (2006, 2007) and Liu et al. (2005, 2009)
Leaf lignin	0:0:1:6	8.6 (2.0)	368:572 (12:57)	38:56 (6:12)	7.9, 7, 0.9	9.3, 7, 0.9	−9.1, 7, 0.6	Couture et al. (2012), Liu et al. (2005, 2009) and Oksanen et al. (2005)
Litter C	0:0:0:3	7.7 (1.2)	357:557 (6:6)	42:63 (6:12)	−1.6, 3, 0.4	0.9, 3, 0.3	−1.1, 3, 0.7	Hillstrom et al. (2010) and Liu et al. (2005)
Leaf N	0:0:3:11	10.0 (2.0)	372:595 (12:88)	35:51 (9:15)	−8.4, 14, 0.7	−6.5, 14, 0.7	−10.9, 14, 0.7	Agrell et al. (2005), Couture et al. (2012), Hillstrom et al. (2010), Kasurinen et al. (2006), Liu et al. (2005), Oksanen et al. (2005) and Talhelm et al. (2012)

TABLE 9.3 Effects of Elevated Atmospheric CO_2 and Tropospheric O_3 on Selected Litter Biochemical and Decomposition-Related Soil Parameters for Young (5 Years or Less) and Intermediate (6–12 Years) Age Trees and Forest Stands—Cont'd

Parameter	Observations GC:GH:OT: FC	Age (years)	A:E CO_2 exp. (ppm)	A:E O_3 exp. (ppb)	eCO_2 (%, *n*, CV)	eO_3 (%, *n*, CV)	$eCO_2 \times eO_3$ (%, *n*, CV)	Sources
Leaf C/N	0:0:2:4	9.0 (1.8)	378:633 (15:113)	32:57 (14:24)	12.5, 6, 0.4	14.5, 6, 0.6	15.7, 6, 0.6	Couture et al. (2012), Kasurinen et al. (2007) and Liu et al. (2005)
Fine root condensed tannins	0:0:0:3	6.5 (0)	360:560 (0:0)	45:70 (0:0)	−34.0, 3, 0.4	−16.8, 3, 0.2	−49.2, 3, 0.7	Chapman et al. (2005)
Fine root lignin	0:0:0:3	6.5 (0)	360:560 (0:0)	46:70 (0:0)	58.5, 3, 0.9	21.0, 3, 0.4	53.6, 3, 1.0	Chapman et al. (2005)
Fine root N	0:0:0:3	6.5 (0)	360:560 (0:0)	46:70 (0:0)	−5.6, 3, 0.9	−5.9, 3, 0.8	−12.1, 3, 0.5	Chapman et al. (2005)
Fine root C/N	0:0:0:3	6.5 (0)	360:560 (0:0)	46:70 (0:0)	11.7, 3, 0.2	−4.1, 3, 0.8	15.7, 3, 0.6	Chapman et al. (2005)
Litter decomposition (MRT)	0:0:0:2	6 (0)	360:560 (0:0)	46:70 (0:0)	0.7, 2, 0.4	12.3, 2, 0.1	5.0, 2, 0.3	Liu et al. (2009)
Soil carbon	0:0:0:3	11 (0)	360:560 (0:0)	46:70 (0:0)	1.5, 3, 0.5	5.4, 3, 0.9	−11.3, 3, 1	Talhelm et al. (2009)

No data were available from mature trees. 'Observations' refers to the number of observations from facilities of the following types: GC, growth chamber; GH, green house; OT, open-top chamber; FC, FACE. Age, A:E CO_2 and O_3 exposures consist of the mean for ambient:elevated levels of CO_2 and O_3 and respective standard deviations.

and as 'intermediate', for 6–20 years of age. We searched the literature for studies of 'mature' trees, 20 years of age or older, but found none. The longest running study was 12 years. The literature was searched until no new sources were identified; then summary statistics (mean, n, SD, CV) were calculated from statistically significant relative responses reported for each parameter across studies (Tables 9.1–9.3). Linear regression was used to test correlations between parameter relative responses and tree age and eCO_2/eO_3 exposure level. Formal meta-analysis was not performed due to a paucity of data for many variables.

9.3   FOREST RESPONSES TO INTERACTING eCO_2 AND eO_3

9.3.1   Experimental Design, Duration and Exposure Regimes

The availability of data varied widely, from a low of 1 observation for parameters such as fine root turnover (FRT) and fine root longevity, to a high of 31 for stem/wood biomass (Tables 9.1–9.3). The total number of observations was greatest from FACE experiments (176), followed by open-top chambers (104), growth chambers (88) and then greenhouses (29) (Tables 9.1–9.3). At first glance, one might expect the smaller-scale less-expensive experimental platforms to be the most widely reported, but the abundance of FACE/OTC observations speaks of the importance and efficiency of such large-scale, multi-investigator, multi-year experiments. The average length of experiments for young systems was 3.3 years, but this was highly variable, with some studies as short as 0.2 years and the longest over 5.0 years. For intermediate systems, the mean age was 7.7 years, but again this was variable with the shortest studies running for 6.0 years and the longest single experiment, the Aspen FACE Project, running for 12.0 years. Although there have been several experiments of eCO_2 and eO_3 alone on mature forest trees (Körner et al., 2005; Matyssek et al., 2006, 2010; Pretzsch et al., 2010), there have been no $eCO_2 \times eO_3$ experiments, leaving a corresponding gap in our knowledge on the effects of this interaction on advanced-age ecosystems. The mean (SD) reported ambient CO_2 concentration was 347 (17) ppm, and that for eCO_2 was 603 (81) ppm, with the variance generally being very low. The mean (SD) ambient O_3 concentration was 34.8 (12) ppb and that for eO_3 was 70.1 (29) ppb, with proportionally much larger variance, perhaps indicating the difficulty of maintaining uniform O_3 target concentrations relative to eCO_2, or more variable background conditions. Although seasonal mean treatment concentrations may not be the most meaningful estimate of exposure or dose, they were the most reliably reported metric and therefore the best basis for comparison between experiments.

9.3.2   Tree Physiology (Gas Exchange and Water Relations)

We focused on the following traits, which were most widely reported in the literature, and are important determinants of leaf- and canopy-level carbon and

water fluxes: net photosynthesis (A_{CO_2}, μmol CO_2 m^{-2} s^{-1}), stomatal conductance (g_s, mmol H_2O m^{-2} s^{-1}), instantaneous water use efficiency (iWUE, μmol CO_2 mmol^{-1} H_2O) and leaf area index (LAI, m^{-2} m^{-2}). We attempted to find information on stand-level transpiration (E, mm year^{-1}) and stand-level WUE (mg biomass produced m^{-3} water transpired year^{-1}), but were unsuccessful. A_{CO_2} and g_s were the most abundant data types (Table 9.1).

In young trees, eCO_2 stimulated A_{CO_2} (+23%) while eO_3 reduced it (−13%) (Table 9.1). Ozone decreased A_{CO_2} by reducing carboxylation efficiency and increasing respiratory costs associated with detoxification and repair processes (Kolb and Matyssek, 2001). Under $eCO_2 \times eO_3$, A_{CO_2} increased by 13%. Therefore, while eO_3 compromised the response of A_{CO_2} to eCO_2, the negative effects of eO_3 were largely ameliorated by eCO_2. Importantly, the absolute response of A_{CO_2} to each treatment varied by about 50%, illustrating the somewhat broad range of responses of A_{CO_2} to eCO_2 and eO_3 in young trees. The effects of eCO_2, eO_3 and $eCO_2 \times eO_3$ on A_{CO_2} were more pronounced in intermediate-aged trees than in young trees, counter to our expectation, with eCO_2 alone stimulating A_{CO_2} by nearly 45% (Table 9.1), which may be an indication that the larger trees, often grown in unrestricted soil in the field, experienced less co-limitation of eCO_2 responses by other factors (Thomas and Strain, 1991). Elevated O_3 reduced A_{CO_2} by a similar magnitude to that observed in young trees (−14%). Interestingly, in intermediate-aged trees growing under $eCO_2 \times eO_3$, A_{CO_2} remained 35% higher than control trees, which demonstrated that eCO_2 more than counteracted the negative effects of eO_3 on leaf carbon gain. Variation in the absolute response of A_{CO_2} to each treatment was small, with CV between 0.10 and 0.20. We found no studies which measured A_{CO_2} under $eCO_2 \times eO_3$ in mature trees. Regardless of tree size or age, it is more likely that trees (i.e. species, genotypes) with higher g_s will have the highest negative response to eO_3 (Herbinger et al., 2007; Kolb and Matyssek, 2001; Reich, 1987; Volin et al., 1998).

Young trees showed consistent reductions in g_s under all treatments, that is, eCO_2, eO_3 and $eCO_2 \times eO_3$ (Table 9.1). The reduction in g_s under $eCO_2 \times eO_3$ was effectively equivalent to the reduction in g_s under eCO_2 alone. Similarly, Medlyn et al. (2001) found a reduction in g_s under eCO_2 (−21%) across different aged trees and species. Despite the consistent reductions in g_s across treatments, variation in g_s was somewhat high (CV~0.60), again demonstrating the wide range of stomatal responses among species and studies. Remarkably, we found only two data points for g_s measured on intermediate-aged trees growing under $eCO_2 \times eO_3$ (Kets et al., 2010). Although the CVs for g_s were low across treatments, sparse data limit our ability to make broad inferences. In any case, g_s decreased by 24% under $eCO_2 \times eO_3$ in intermediate-age trees, similar to the g_s reduction in young trees under that treatment. Again, we found no g_s data for mature trees growing under $eCO_2 \times eO_3$. Interestingly, these data show that reductions in g_s under eCO_2 and eO_3 are relatively similar across tree ages, with g_s more affected by eCO_2 than eO_3 (Table 9.1). Moreover, these data

generally match the 21% reduction in g_s under eCO$_2$, reported by meta-analysis (Medlyn et al., 2001).

From studies which report both A_{CO_2} and g_s, we estimated iWUE (A_{CO_2}/g_s). The standard model suggests that eCO$_2$ increases iWUE (Ellsworth et al., 1995; Long et al., 2004) and eO$_3$ reduces iWUE (Kolb and Matyssek, 2001). Data from the current literature survey show that eCO$_2$ increased iWUE similarly across tree ages (+69–88%), and eO$_3$ had little to no effect, regardless of tree age (Table 9.1); however, there is evidence that mature trees may respond differently (Kitao et al., 2009; Löw et al., 2006). It was seen that iWUE increased substantially under eCO$_2 \times$ eO$_3$ in young and intermediate-aged trees. Compared to A_{CO_2} and g_s, iWUE showed the lowest CVs suggesting a more consistent pattern of responses to eCO$_2$. Overall, these results do not suggest that eCO$_2$ ameliorates the negative effects of eO$_3$ on iWUE because eO$_3$ had little effect on iWUE in the studies reviewed here (but see Matyssek and Sandermann, 2003).

Interestingly, we found only three data points reporting LAI of young trees growing under eCO$_2 \times$ eO$_3$. Although the data are minimal, they suggest that eCO$_2$ stimulates LAI (+15%), eO$_3$ reduced LAI (−18%) and eCO$_2$ does not ameliorate the negative effects of eO$_3$ on LAI in young trees (Table 9.1). Intermediate-aged trees show similar responses to eCO$_2$ and eO$_3$, but this was again more pronounced; LAI increased more with eCO$_2$, and decreased more with eO$_3$. Moreover, although the data were limited to one study (Uddling et al., 2008), LAI increased by 6% under eCO$_2 \times$ eO$_3$. The results from young and intermediate-age trees suggest that eO$_3$ severely limits increased LAI under eCO$_2$.

Data on stand-level E and WUE under eCO$_2 \times$ eO$_3$ were non-existent and there is generally little information on canopy-level processes in older stands exposed to either eCO$_2$ or eO$_3$. This gap in the data makes it difficult to examine how ontogeny influences *canopy-level* responses to eCO$_2$ and eO$_3$. Studies by Uddling et al. (2008, 2009) provide the most insight into stand-level water use under eCO$_2 \times$ eO$_3$. Their results suggest that eO$_3$ does not significantly affect tree water use and canopy conductance, but rather, eCO$_2$ increases tree water use because of increased growth and leaf area. Similarly, Tricker et al. (2009) found that eCO$_2$ did not reduce stand water use because eCO$_2$ increases the amount of transpiring leaf area. Thus, water use at the leaf and canopy level may show very different responses to eCO$_2$. However, in agreement with leaf-level responses, Ellsworth et al. (1995), Wullscheger and Norby (2001) and Wullscheger et al. (2002) found reduced stand water use under eCO$_2$, although not of the same magnitude of leaf-level responses, most likely due to issues of scale and environmental variability. Notably, it is hypothesized that eCO$_2$ increases stand-level WUE, yet we found only one study which estimated stand-level WUE under eCO$_2$ (Wullscheger and Norby, 2001). Wullscheger and Norby (2001) found that eCO$_2$ increased stand-level WUE. Clearly, the data on canopy-level responses to eCO$_2$ and

eO_3 alone, and more so as $eCO_2 \times eO_3$, are extremely limited and sometimes contradictory, making it difficult to identify response trends and predict forest ecosystem responses to interacting eCO_2 and eO_3.

Lastly, it has been noted that ontogeny be considered when examining the effects of eCO_2 and eO_3 on forest ecosystems (Chappelka and Samuelson, 1998; Matyssek et al., 2010; Norby et al., 2005). Mature and young trees are structurally different and have different rates of water and nutrient uptake, which ultimately determine their response to eCO_2 and eO_3. As reviewed by Chappelka and Samuelson (1998), seedlings often have greater g_s, which results in higher O_3 uptake and greater reductions in A_{CO_2}, compared to mature trees. For many of the same reasons, young trees may be more responsive to eCO_2 (Medlyn et al., 2001). Furthermore, under $eCO_2 \times eO_3$, responses that were significant at young ages (Noormets et al., 2001) may no longer be significant as trees mature (Uddling et al., 2009). Based on our analysis, under interacting eCO_2 and eO_3, A_{CO_2}, iWUE and LAI were less compromised by eO_3 in intermediately aged trees than young trees, and g_s showed similar responses to $eCO_2 \times eO_3$ across tree age groups. While there were no studies on mature trees in this survey, this trend suggests that the positive effects of eCO_2 become more pronounced with age while the negative effects of eO_3 may become less. However, much of the data on physiological processes has been collected on young trees in growth chamber experiments with biotic and abiotic stress agents excluded (Ainsworth and Long 2005; Matyssek et al., 2010). Thus, in terms of physiological processes, important questions remain with regard to how mature forests growing in natural conditions respond to interacting $eCO_2 \times eO_3$, and much is yet to be learned regarding stand-level E and WUE being affected by $eCO_2 \times eO_3$ (Karnosky et al., 2003, 2005; Matyssek et al., 2010; Pretzsch et al., 2010). More extensive, long-term FACE-type experiments in mature forest ecosystems will provide the most insight into forest ecosystem responses to atmospheric change.

9.3.3   Biomass and Net Primary Production

Biomass and net primary production (NPP) data for both young and intermediate-age trees consisted of foliage, stem/wood, coarse root (CR), fine root (FR), FRT or life span, total aboveground biomass (AG), total belowground biomass (BG), total above- and belowground biomass (AGBG), aboveground NPP (ANPP) and total NPP (Table 9.2). Data were more abundant for young ecosystems (mean $n = 15$) compared to intermediate (mean $n = 5$), and in both groups the order of data abundance was generally foliage = stem wood > AG = BG = AGBG > FR > CR > ANPP > FRT = NPP. The exception to this was that fine root biomass data were much more abundant ($n = 11$) than the overall mean in intermediate-age systems. Only one study, the Aspen FACE Project, provided ecosystem-level estimates of ANPP and NPP (King et al., 2005; Zak et al., 2011; Pregitzer and Talhelm, this volume).

As with the broader ecological literature, data on FRT were very limited, restricted to only two studies but using a total of 5 years of root observation data from minirhizotrons (Phillips et al., 2009; Pregitzer et al., 2008). Therefore, our knowledge of these key components of terrestrial C cycling as affected by the eCO$_2$ × eO$_3$ interaction remains very basic.

Elevated CO$_2$ was generally a highly significant factor that stimulated biomass production of all plant parts in both young and intermediate-age trees in the studies surveyed. The mean stimulation due to eCO$_2$ across all parameters in young trees was 29.6% relative to the control, with a low of 18.4% for foliage and a high of 41.8% for fine roots. The variance of these responses, as estimated by the coefficient of variation, ranged from 0.43 for ANPP to 1.24 for foliage, reflecting the fact that the former was estimated from a single study using uniform methods while the latter came from many different studies. The mean stimulation due to eCO$_2$ relative to the control in intermediate-age trees was 36.7%, with a low of 2.8% for FRT and a high of 53.7% for fine root biomass. This was contrary to our expectation that younger trees or forest ecosystems would have higher responsiveness to eCO$_2$. Although based on fewer observations, the CV for intermediate-age tree responses was less than for young trees (mean of 0.7 compared to 0.8), which again could be related to the smaller sample size, but also may suggest that responses become more consistent through time. The magnitude of the stimulation due to eCO$_2$ overall, and the relatively high responsiveness of fine roots in particular are consistent with the broader eCO$_2$ literature (Curtis and Wang, 1998; Dieleman et al., 2012; Norby et al., 2005).

Elevated O$_3$, also generally highly significant, decreased biomass production almost universally across parameters, although exceptions occurred related to fine roots in both young and intermediate-age trees (Table 9.2). The mean decrease in biomass production in young trees relative to the control was −12.5%, with the most responsive parameter being total belowground biomass (−19.1%) and the least being CRs (−2.7%). The CV of these responses averaged 1.65, more than double that for eCO$_2$. For intermediate-age trees, the decrease in biomass production due to eO$_3$ relative to the control averaged −15.0%, which as for eCO$_2$, was greater than the mean response of young trees. The CV of the mean decrease in biomass production (0.65) was much lower than for young trees. Again, this could be a function of fewer observations or less variable responses in older trees. Interestingly, fine root biomass in intermediate-age trees showed a mean stimulation due to eO$_3$ of 1.82% relative to the control, but this was accompanied by a CV of 8.08. The extremely large variance occurred because of the 11 observations, 6 were negative (average of −20.4%) and 5 were positive (average of 28.5%). FRT was stimulated by eO$_3$ relative to the control in both young (5.0%) and intermediate (2.8%) age trees, but the data were from a single study in each case. Clearly, fine roots are highly responsive to eO$_3$ but the direction of response is variable across ecosystems, age classes and environmental conditions. At the Aspen FACE project,

the pure aspen community showed a consistent stimulation in fine root biomass under eO$_3$ over time (King et al., 2005; Pregitzer et al., 2008; Rhea and King, 2012), whereas the aspen-birch and aspen maple communities did not, suggesting a strong genetic effect on ecosystem function. A later analysis (Zak et al., 2011) incorporated estimates of turnover with the fine root biomass and estimated a non-significant 8% *increase* in total NPP in the aspen community in the 12th year of the experiment. That fine root dynamics can have such a large impact on total NPP, and potentially net ecosystem productivity (NEP), in response to air pollution illustrates the continuing need for a much better understanding of belowground processes (see also Kraigher et al., this volume).

Finally, in the experiments surveyed, the eCO$_2$ × eO$_3$ interaction was generally not statistically significant and resulted in positive stimulation of all biomass production parameters in both young and intermediate-age trees relative to the control (Table 9.2). This suggests that the effects of eCO$_2$ and eO$_3$, when occurring together, are generally additive, and that the positive effects of eCO$_2$ more than offset the negative effects of eO$_3$ on biomass production. This is consistent with the magnitude of the relative responses for eCO$_2$ and eO$_3$ treatments when applied alone. The mean stimulation in biomass in the eCO$_2$ × eO$_3$ treatment, relative to the control across parameters, was 15.1% in young trees, with a mean CV of 2.16, which is a higher variance than for eCO$_2$ and eO$_3$. In intermediate-age trees, the mean increase across biomass production parameters in the eCO$_2$ × eO$_3$ plots relative to the control was 20.1%, with a mean CV of 0.82. Again, a larger relative treatment response in intermediate compared to young trees is counter to our expectation, and the lower variance suggests a smoothing out of responses through time or a narrower range of variation in responses due to fewer studies. The most responsive parameter was again fine root biomass with increases under eCO$_2$ × eO$_3$ of 37.1% and 47.8% in young and intermediate-age trees, respectively. The least responsive parameters were FRT (0%) and total belowground biomass (3.6%) relative to control in young trees, and total NPP (0%) in intermediate-age trees, but the ability to make inferences is limited by the small number of studies.

9.3.4 Litter Decomposition and Soil Relations

The parameters for litter biochemistry surveyed include condensed tannins (mg/g), total soluble phenolics (mg/g), lignin (mg/g), C (mg/g), N (mg/g) and C/N for leaf and fine root litter. The parameters for soil carbon cycling include litter mean resident time (MRT, year), which represents litter decomposition rate and total soil carbon (g/m^2). Most of the data were from studies conducted in young tree systems with ages ranging from 1 to 5 years, and intermediate tree systems with ages ranging from 6 to 12 years. As with physiology and biomass production, no data were available for mature (>20 years of age) tree/forest systems (Figure 9.1).

FIGURE 9.1 Researchers collect leaf litter for biochemical analysis and to estimate litter biomass production using mesh-lined baskets (left) and recover field incubation bags of foliage and fine root litter (right) to estimate decomposition dynamics as affected by the $eCO_2 \times eO_3$ interaction at the Aspen FACE Experiment in Rhinelander, Wisconsin, USA. *Photo credit: John King.*

Growth of trees under eCO_2 generally increased the concentrations of secondary metabolites in leaves. In leaf litter of young and intermediate-age trees, eCO_2 increased the concentrations of condensed tannins by a mean of 15.5% and 19.6%, respectively, and increased the concentration of total soluble phenolics by a mean of 8.9% and 14.6%, respectively. Although most of the individual studies included in this review did not detect a significant effect, the overall mean response of lignin to eCO_2 was positive in leaf and fine root litter. Elevated CO_2 increased lignin concentration by 5% and 7.9% in leaf litter of young and intermediate trees, respectively, and by 58.5% in fine root litter of intermediate-age trees. The increases in the concentrations of secondary metabolites under eCO_2 can be explained on the basis of growth-differentiation balance hypothesis (Herms and Mattson, 1992). Elevated CO_2 increases production of carbohydrates but plant growth does not increase proportionally because of limited soil nutrient supply (Luo et al., 2004). Elevated CO_2 therefore leads to more carbohydrates allocated to secondary metabolic pathways.

The responses of condensed tannins, phenolics and lignin to eO_3 were different for young and intermediated age trees. In young trees, eO_3 had a small impact on the concentration of condensed tannins, but decreased phenolics (-9.9%) and lignin (-15.4%) concentration in leaf litter. In intermediate-age trees, eO_3 increased the concentrations of condensed tannins by 34.1%, phenolics by 26.3% and lignin by 7.9% in leaf litter. The different response between young and intermediate-age trees was probably due to shifts in carbon allocation strategy from growth to defence in older trees. It has been shown that eO_3 depresses photosynthesis but triggers anti-oxidant defence responses (Kangasjarvi et al., 1994). In young trees, as lower carbohydrate supply constrains allocation to secondary metabolism, eO_3 had small or negative impacts on the synthesis of secondary metabolites. With tree growth, the up-regulation of the shikimic acid pathway leads to an increase in anti-oxidants under elevated O_3 (Lindroth, 2010), that may explain the higher condensed tannin and phenolic concentrations in leaf litter (Lindroth, 2010; Matyssek et al., 2013; Couture and Lindroth, 2013; Pregitzer and Talhlem, 2013, this vol.).

In addition to altering the concentrations of secondary metabolites, eCO_2 also tended to decrease N concentration in leaf and fine root litter, with leaf litter showing a greater response (-14.2% and -8.4% for young and intermediate trees, respectively) than fine root litter (-2.6% and -5.6% for young and intermediate trees, respectively). Lower N concentration was accompanied by higher C/N ratio in leaf and fine root litter for both young and intermediate-age trees. It has been shown that eCO_2 often leads to an accumulation of carbohydrates, especially starch, in leaves (Lindroth, 2010). The dilution effect of increased carbohydrates therefore resulted in a lower N concentration and higher C/N ratio in leaf litter. Elevated O_3 showed a similar reduction in N concentration. Leaf and fine root litter grown under eO_3 had lower N concentration and higher C/N ratio, except for fine root litter of young trees, which increased by a mean of 4.6%.

Most studies included in this review found that the interaction of eCO$_2$ and eO$_3$ was not statistically significant for leaf chemistry changes (Chapman et al., 2005; Holton et al., 2003; Kasurinen et al., 2006; Liu et al., 2005; see also Chapters 11 and 15). Litter chemistry under the eCO$_2 \times$ eO$_3$ treatment was therefore often influenced by the additive effects of eCO$_2$ and eO$_3$. Compared to eCO$_2$ or eO$_3$ only treatments, eCO$_2 \times$ eO$_3$ treatment resulted in greater increases in the concentrations of condensed tannins, phenolics and C/N, and a greater decrease in N concentration (Table 9.3).

The changes in litter quality under eCO$_2$ and eO$_3$, such as increases in condensed tannins, phenolics and C/N, are expected to lead to lower decomposition rates. Mean responses found here suggest that eCO$_2$ decreased litter decomposition in both young and intermediate tree systems, while eO$_3$ stimulated litter decomposition in young tree systems but reduced it in intermediate tree systems (Table 9.3). However, the changes in litter decomposition were usually not significant in individual experiments, or the impacts were often transient. For example, Liu et al. (2009) found eO$_3$ decreased litter mass loss only in the first year, but not in the second year. In an OTC experiment, Kasurinen et al. (2006) found that litter decomposition was not affected by eO$_3$ exposure in the first 2 years, but a slower decomposition rate was found in the third year of incubation.

All data on changes in soil C were from only two studies conducted at the Aspen FACE Project at different stages of stand development (Loya et al., 2003; Talhelm et al., 2009). Although the mean responses showed eCO$_2$ and eO$_3$ altered total soil carbon in young and intermediate tree systems (Table 9.3), the changes were not statistically significant (Talhelm et al., 2009). The 11-year study at Aspen FACE indicated that the effects of eCO$_2$ and eO$_3$ on soil C varied with stand development. After the first 4 years of fumigation at the Aspen FACE, Loya et al. (2003) found that the formation of new soil carbon under eCO$_2 \times$ eO$_3$ treatment was 51% less than that under eCO$_2$-only treatment. However, a later study by Talhelm et al. (2009) suggested that the initial reduction in new C accumulation in eO$_3$ under eCO$_2$ was only a temporary effect. The amount of new soil C under the eCO$_2$ and eCO$_2 \times$ eO$_3$ appears to have converged in the fifth year of the experiment. After 11 years of fumigation, neither eCO$_2$ nor eO$_3$ induced significant impacts on new soil carbon accumulation or total soil carbon content. As with estimates of NPP, however, inferences on the effects of the eCO$_2 \times$ eO$_3$ interaction on soil C formation are necessarily limited by the lack of data.

9.4   SUMMARY OF PHYSIOLOGY, BIOMASS PRODUCTION AND SOC CYCLING RESPONSES TO eCO$_2 \times$ eO$_3$

We were able to locate 58 studies published between 1990 and 2012 reporting primary data on forest tree physiology, biomass production, litter quality and decomposition responses from eCO$_2 \times$ eO$_3$ interaction experiments. Studies

were abundant for young trees (<6 years) from growth chamber, greenhouse and OTC experiments. As might be expected, longer-term studies on intermediate-age trees (6–12 years) were less abundant and primarily from OTC and FACE experiments. We found that no $eCO_2 \times eO_3$ studies have been conducted on mature forest trees (>20 years). This represents a large gap in our knowledge of forest response to air pollution and climate change because we know that physiological and ecosystem functional processes change through stand development, leaving this important interaction unrepresented for much of the world's forests. Data on leaf-level photosynthesis, stomatal conductance, foliage, fine root and aboveground biomass, and leaf/litter N concentration were most abundant, but were severely lacking for many other parameters important to the storage and cycling of C, water and nutrients in forest ecosystems. In particular, our knowledge of canopy-scale processes (evapotranspiration, gross primary production, net ecosystem exchange), belowground C inputs to soil (fine root production and turnover) and changes in SOC formation is particularly limited, yet these are some of the most important processes to understand.

There were commonalities in how eCO_2 and eO_3, alone and in combination, affected physiology, biomass production and litter decomposition, and the net effect of the $eCO_2 \times eO_3$ interaction was fairly consistent. In terms of physiology, there was a strong positive response of A_{CO_2} to eCO_2 and a negative response to eO_3 that was more than compensated for under $eCO_2 \times eO_3$ (i.e. a net increase relative to control). Stomatal conductance was strongly decreased by eCO_2 but not greatly affected by eO_3; hence, the $eCO_2 \times eO_3$ treatment was similar to eCO_2. Instantaneous WUE therefore increased under eCO_2 with and without simultaneous exposure to eO_3. Leaf area index increased under eCO_2, decreased with eO_3 and showed slight increase with $eCO_2 \times eO_3$. For most physiological parameters, responses of intermediate-age trees were greater than in young trees, which was counter to expectation. In terms of biomass production, there were generally strong positive and strong negative responses to eCO_2 and eO_3, respectively. As with physiology, the net effect of the $eCO_2 \times eO_3$ interaction was generally not statistically significant, but still important to quantify because relative responses (relative to control) were generally intermediate compared to eCO_2 and eO_3 when applied alone. Few studies reported significant effects of eCO_2 or eO_3 on biomass partitioning (data not shown), and as for physiology, ontogenetic effects were counter to expectation: that is, relative responses were greater and less variable for intermediate-age compared to young trees. Linear regression did not reveal any significant correlations of relative responses versus age or exposure level, which could be due to limited data available.

Finally, in terms of SOC cycling, concentrations of secondary metabolites (condensed tannins, soluble phenolics and lignin) generally increased in response to eCO_2, and responses were again larger in intermediate-age compared to young trees. Interestingly, eO_3 decreased concentrations of secondary metabolites in young trees but increased them in intermediate-age trees,

perhaps indicating a shift in C allocation from growth to defence with age. Litter N concentration decreased with both eCO_2 and eO_3, except for young fine root litter, in which it increased with eO_3. Changes in litter quality may be expected to change decomposition dynamics, and the data of our survey suggest that eCO_2 decreased litter decomposition in both young and intermediate tree systems, while eO_3 stimulated litter decomposition in young tree systems but decreased it in intermediate-age systems. However, the changes in litter decomposition were usually not significant in individual experiments, or the impacts were often small or transient. Data on SOC from long-term studies were extremely limited (only one study longer than 5 years), but suggest little significant effect due to eCO_2 or O_3, alone or in combination. The above conclusions should be tempered by the realization that most studies reviewed here were performed on young plants under highly controlled conditions, often with abundant water and nutrients. More work is needed to determine long-term forest responses to eCO_2 and eO_3, especially in older age classes, and as affected by interacting biotic and abiotic environmental stresses.

9.5   MOVING FORWARD

In closing, we may ask: What are the most pressing scientific questions remaining on forest responses to interacting eCO_2 and eO_3? and How can science best be used to inform policy to enhance social welfare? A good illustration of science and policy working together is research that showed the potential for eO_3 to decrease forest productivity in response to eCO_2 in young north-temperate forests (Isebrands et al., 2001; Karnosky et al., 2003; King et al., 2005), which if representative, could imply air pollution limitation of the capacity of the world's forests to counteract the build-up of atmospheric CO_2. This science supported the decision to decrease the secondary air quality standard for O_3 in the United States (U.S. Federal Register, 27 March 2008), with resulting health benefits for humans and vegetation. However, how widespread this productivity response is, whether the key processes governing C storage act uniformly across forests and stages of stand development and how they interact with other environmental stresses (e.g. drought) is still very poorly understood. Clearly, this survey has demonstrated that data for most important C cycling processes, especially for later stages of forest development, are very limited. There simply have not been enough long-term, large-scale experiments, which incidentally are also some of the most efficient in terms of scientific output for the resources invested. Critical data gaps remain for canopy-level processes affecting C assimilation and water cycling, belowground processes affecting SOC formation and nutrient dynamics and long-term net ecosystem CO_2 exchange with the atmosphere. Several long-term experiments have successfully demonstrated that exposure of mature forest ecosystems to eCO_2 and eO_3 (individually) is possible using a system of

pressurized tubing to distribute the fumigation gas throughout the forest canopy (Körner et al., 2005; Matyssek et al., 2010; Chapters 1 and 6). This technology promises to provide a lower cost alternative to the more technically challenging forced-air FACE approach to forest fumigation that could facilitate future $eCO_2 \times eO_3$ experiments. Such studies in natural ecosystems are especially important for process-level understanding and model parameterization, and they are technically feasible.

Moving forward, when thinking about future research on interacting air pollution and climate change, and potential development of a distributed network of long-term research 'supersites' (e.g. see Mikkelsen et al., 2013, this vol.), we recommend considering a subset of projects that examine the interaction of eCO_2 and eO_3 over the major stages of stand development in both coniferous and deciduous forests. This review suggests that more information on intermediate-age and mature ecosystems is most urgently needed. Empirical studies should work iteratively with development of process-based ecosystem models to refine mechanistic understanding of ecosystem function and test hypotheses related to future forest responses to climate and air pollution. The improved ecosystem models can then be linked to larger-scale models to extrapolate the interactive effects of $eCO_2 \times eO_3$ on carbon, water and nutrient cycling at the region-to-global scale, and forward in time.

Finally, an argument can be made that current environmental policy lags behind the science we already have at hand, and a goal for the future should be scientifically literate public officials who implement legislation based on sound science in a timely manner. For example, we know well that negative health consequences arise for humans and vegetation when background tropospheric O_3 concentration exceeds 60 ppbv for any length of time, yet the primary and secondary air quality standards for tropospheric O_3 in the United States remain fixed at 75 ppbv. Similarly, there is strong scientific consensus that the rising atmospheric CO_2 concentration is directly linked to the changing climate, yet global CO_2 emissions continue to increase at an increasing rate and development of alternative energy sources proceeds at a snail's pace. This feeds back to our responsibility as educators to develop an educated electorate who will elect public officials who embrace science as the basis of sound policy, and who will hold them accountable for failing to do so. An informed leadership must possess the foresight and courage to invest in the science that will guide development of environmental policy that balances near-term economic welfare and long-term climate stability, environmental quality and sustainability to enhance the quality of life for a rapidly rising population.

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