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INVITED REVIEW

Evidence of current impact of climate change on life: a walk from genes to the biosphere

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Abstract

We review the evidence of how organisms and populations are currently responding to climate change through phenotypic plasticity, genotypic evolution, changes in distribution and, in some cases, local extinction. Organisms alter their gene expression and metabolism to increase the concentrations of several antistress compounds and to change their physiology, phenology, growth and reproduction in response to climate change. Rapid adaptation and microevolution occur at the population level. Together with these phenotypic and genotypic adaptations, the movement of organisms and the turnover of populations can lead to migration toward habitats with better conditions unless hindered by barriers. Both migration and local extinction of populations have occurred. However, many unknowns for all these processes remain. The roles of phenotypic plasticity and genotypic evolution and their possible trade-offs and links with population structure warrant further research. The application of *omic* techniques to ecological studies will greatly favor this research. It remains poorly understood how climate change will result in asymmetrical responses of species and how it will interact with other increasing global impacts, such as N eutrophication, changes in environmental N : P ratios and species invasion, among many others. The biogeochemical and biophysical feedbacks on climate of all these changes in vegetation are also poorly understood. We here review the evidence of responses to climate change and discuss the perspectives for increasing our knowledge of the interactions between climate change and life.

Keywords: biosphere, climate change, community, drivers of global change, drought, ecosystem, evolution, extinction, feedbacks, genomics, genotype, growth, metabolomics, migration, phenology, phenotype, population, warming

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Introduction. Rapid atmospheric and climate change

Elevated concentrations of atmospheric greenhouse gases have changed global climate, raising the Earth's surface temperature by 0.74 °C in the past century (IPCC, 2007). The main cause is the rise in concentration of atmospheric CO_2 from 280 ppm at the beginning of the industrial revolution to the current 394 ppm (Tans, 2012). This rapid rise has few precedents in Earth's history, at least in the last 500 million years (Mora *et al*., 1996; Petit *et al*., 1999; Beerling, 2002). The current rise continues to increase exponentially despite the few global policies aimed at stopping it; (Peñuelas & Carnicer, 2010; Carnicer & Peñuelas, 2012) for example, an increase in 2.36 ± 0.09 ppm of CO_2 in 2010 was one of the largest annual increases in recent decades (Peters *et al*., 2012), suggesting that levels of CO_2 are likely to increase further and at faster rates. The current increase in concentrations of atmospheric CO_2 is equivalent to 71.8 ppm of CO_2 per century, which is several orders of magnitude greater than the rates of CO_2 increase observed in Earth's atmosphere in previous periods of rapid changes in atmospheric CO_2: 0.003–0.012 ppm during the Paleozoic (Mora *et al*., 1996), 0.0075–0.012 ppm during the Cenozoic (Beerling, 2002) or 0.8–1 ppm during the last glaciation (Petit *et al*., 1999). To the current rapid increase in atmospheric CO_2 concentrations, we must add the increases in the concentrations of other greenhouse gases such as methane and nitrogen oxides that are also increasingly emitted

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by human activities (IPCC 2007). This rapid increase in the atmospheric concentrations of CO_2 and other greenhouse gases has the potential to drive current climatic changes more quickly than all previous climatic changes (IPCC 2007). These rapid changes may exceed the capacities of individuals, populations and communities to assimilate them. Therefore, an immediate key question in the biology of global change is how the Earth-life system is coping with this new situation.

In this study, we review evidence of current biological impacts of climate change, the capacity of terrestrial organisms, populations, communities and ecosystems to cope with current climate change, and the upscaling of their responses, from the molecular and genetic level to the levels of community, ecosystem and biosphere (Fig. 1). We also identify some of the remaining questions warranting further research for better understanding the capacity of terrestrial organisms, populations, communities and ecosystems to adapt to climate change, including the interactions with other drivers of global change, and for better understanding the possible feedbacks on climate of these changes in organisms, populations, communities and ecosystems.

Responses of organisms

Molecular

Several studies have observed important phenotypic responses of organisms to drought and warming at the molecular level (Table 1). Ecometabolomic studies (Sardans *et al.*, 2011; Rivas-Ubach *et al.*, 2012) are a promising approach for gaining knowledge of the molecular plasticity of the responses of organisms to drought and warming. For example, relative to control individuals, *Erica multiflora* plants subjected to drought exhibited increased concentrations of antioxidant compounds, such as quinic and tartaric acid, and of elements such as K, and lower concentrations of sugars, amino acids and P (Rivas-Ubach *et al.*, 2012). These ecometabolomic studies allow the detection of the main metabolic pathways responsible for organismic responses and further help to recognize the genes involved in the response. The application of these emerging *omic* techniques to ecological and ecophysiological studies has already illustrated the large capacity of plants and animals to present plastic molecular responses to drought and warming. Molecular responses of plants to drought include increases in the concentrations of several enzymes as a result of the enhanced expression of some genes responsive to drought (Table 1), in particular the genes of the synthetic pathways of abscisic acid (ABA) and proline, and the mobilization of soluble sugar from stored polysaccharides (Table 1). These changes in gene expression are thereafter related to shifts in metabolomic structure (Alvarez *et al.*, 2008; Selter *et al.*, 2010; Krugman *et al.*, 2011; Sardans *et al.*, 2011; Rivas-Ubach *et al.*, 2012; Spieb *et al.*, 2012; Warren *et al.*, 2012) (Fig. 2). For example, the genes involved in drought tolerance are frequently related to the maintenance of turgor and cell integrity (Chang *et al.*, 1996; Rabello *et al.*, 2008; Foito *et al.*, 2009; Aranjuelo *et al.*, 2011; Erxleben *et al.*, 2012). Some compounds such as proline, phenolics, ABA, gamma aminobutyric acid (GABA) and soluble and alcohol sugars are frequently involved in the responses of plants to drought (Table 1). The mechanisms and molecules stimulated by drought protection, though, are very diverse among different species (Carmo-Silva *et al.*, 2009; Hamanishi & Campbell, 2011; Warren *et al.*, 2012) and even among different genotypes of the same species (Regier *et al.*, 2009; Cohen *et al.*, 2010; Hamanishi *et al.*, 2010; Yang *et al.*, 2010; Saxena *et al.*, 2011; Sanchez *et al.*, 2012; Warren *et al.*, 2012).

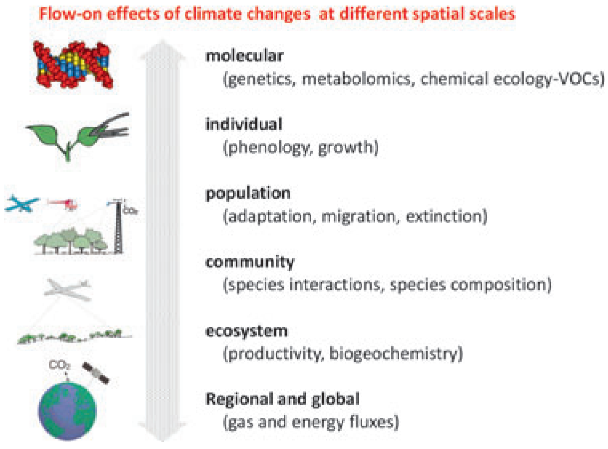

Fig. 1 Impacts from climate change on life at different spatial scales from the molecular to the biospheric levels.

Similarly, individual plants also change molecular composition in response to warming. *Omic* studies have revealed higher levels of expression of some genes (Zhang *et al.*, 2005a) and increased synthesis of some heat-stress proteins (Table 1) and of other metabolites and in other metabolic pathways (Guy *et al.*, 2008; Sardans *et al.*, 2011) (Table 1). Some studies suggest an increase in some pathways of protein catabolism linked to a rise in the synthesis of protective antistress proteins (Xu & Huang, 2008a,b, 2010; Xu *et al.*, 2008). Other studies show changing genotypic compositions at the population level in response to drought and/or warming (Jump *et al.*, 2006a, 2008).

The mechanisms of molecular responses to warming strongly differ when comparing different plant species, even those belonging to the same genus (Xu & Huang,

Table 1 *Omic* studies that have analyzed phenotypic responses to drought and warming at the molecular level

Species	Analytical techniques used	Principal results	References
Molecular responses of organisms to DROUGHT			
Capsicum annuum	Target metabolomics (HPLC-UV)	↑ Phenolics	Estiarte *et al.* (1994)
Zea mays	Metabolomics (HPLC-MS/MS)	↑ Threonine, GABA, 6-benzylaminopurine, proline, tryptophan, leucine	Alvarez *et al.* (2008)
Medicago sativa	Metabolomics (GC-MS)	↑ Proline, *p*-pinitol	Aranjuelo *et al.* (2011)
Eucalyptus sp.	Metabolomics (capillary GC)	↑ Carbohydrates, quercitol, polyols	Arndt *et al.* (2008)
Cynodon dactylon, *Zoysia japonica*	Metabolomics (GC-MS)	↑ 5-hydroxynorvaline	Carmo-Silva *et al.* (2009)
Pisum sativum	Metabolomics (^{1}H NMR)	↑ Proline, valine, threonine, homoserine, myoinositol, GABA	Charlton *et al.* (2008)
Vitis vinifera	Metabolomics (GC-MS)	↑ Glucose, maltose, proline	Cramer *et al.* (2007)
Physcomitrella patens	Metabolomics	↑ Proline, altrose, maltitol, ascorbic acid	Erxleben *et al.* (2012)
Lolium perenne	Metabolomics (GC-MS)	↑ Glucose, raffinose, fructose, trehalose, maltose ↓ Fatty acids	Foito *et al.* (2009)
Oryza sativa	Metabolomics (^{1}H NMR)	↑ Glucose, glutamate, glutamine	Fumagalli *et al.* (2009)
Stagonosphera nodorum	Metabolomics (GC-MS)	↑ Glycerol, arabitol ↓ Several amino acids	Lowe *et al.* (2008)
Arabidopsis sp.	Metabolomics (^{1}H NMR, HPLC-UV)	↑ Proline, tyrosine, malate, GABA	Lugan *et al.* (2009)
Solanum tuberosum	Metabolomics	↑ Sucrose, trehalose	Mane *et al.* (2008)
Belgica antartica	Metabolomics (GC-MS)	↑ Glycerol, erythritol, serine	Michaud *et al.* (2008)
Lupinus albus	Metabolomics (^{13}C NMR)	↑ Sucrose, glucose, proline	Peuke & Rennenberg (2004)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Sucrose, maltose, glucose, proline	Rizhsky *et al.* (2004)
Erica multiflora	Metabolomics (^{1}H NMR)	↑ Polyphenolics, quinic acid, choline, tartaric acid	Rivas-Ubach *et al.* (2012)
Lotus sp.	Metabolomics (GC-MS)	↑ Proline, sugars ↓ Aspartic acid, glutamic acid, serine, threonine	Sanchez *et al.* (2012)
Solanum sp.	Metabolomics (GC-MS)	↑ Alanine, GABA, β-alanine, homoserine, isoleucine, proline, serine, valine ↓ Glutamine, glycine, cysteine	Semel *et al.* (2007)
Eucalyptus sp.	Metabolomics (GC-MS)	↑ Sugars and sugar alcohols but in different intensities in different species	Warren *et al.* (2012)
Medicago sativa	Metabolomics(HPLC)	↑ Sucrose, succinate, malate	Naya *et al.* (2007)
Gossypium hirsutum	Metabolomics	↑ Several amino acids, proline, polyphenols	Parida *et al.* (2007)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Several amino acids and raffinose	Urano *et al.* (2009)
Oriza sativa	Proteomics	22 proteins associated with drought tolerance were identified	Rabello *et al.* (2008)
Quercus robur	Proteomics	18 proteins associated with drought tolerance were identified	Sergeant *et al.* (2011)
Glycine max	Proteomics	5 proteins increased and 21 decreased under drought	Alam *et al.* (2010)
Populus × *euramericana*	Proteomics	↑ Antioxidant proteins	Bonhomme *et al.* (2009)
Populus sp.	Proteomics	↑ Proteins associated with photosynthesis and some protein families related to cellular water transfer ↓ Some protein families related to cellular water transfer	Plomion *et al.* (2006)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Medicago sativa	Proteomics	↑ Rubisco protein	Aranjuelo *et al.* (2011)
Oryza sativa	Proteomics	↑ Superoxide dismutase	Muhammad Ali & Komatsu (2006)
Pinus armandii	Proteomics	5 proteins changed their concentrations under drought	He *et al.* (2007)
Populus sp.	Proteomics	↑ Rubisco protein ↓ Membrane-related proteins	Durand *et al.* (2011)
Quercus ilex	Proteomics	↑ Triosephosphate isomerases, rubisco activase ↓ Peroxidase	Echevarría-Zomeño *et al.* (2009)
Populus kangdingensis	Proteomics	↑ Proteins related to redox homeostasis and sugar metabolism	Yang *et al.* (2010)
Populus × *euramericana*	Proteomics	↓ Proteins related to photosynthesis	He *et al.* (2008)
Populus cathayana	Proteomics	↑ Proteins related to antithermal stress, secondary metabolism and defense	Xiao *et al.* (2009)
Triticum aesticum	Proteomics	↑ Some globulin, gliadin and albumin proteins	Yang *et al.* (2011)
Triticum aesticum	Proteomics	↑ Expression of 36 proteins	Caruso *et al.* (2009)
Populus cathayana	Proteomics	↓ Proteins related to photosynthesis	Zhang *et al.* (2010a)
Carissa spinarum	Proteomics	↓ Proteins related to photosynthesis	Zhang *et al.* (2010b)
Solanum tuberosum	Transcriptomics	↑ Raffinose and proline synthesis pathways ↓ Superoxide dismutase synthesis	Mane *et al.* (2008)
Lolium perenne	Transcriptomics	↑ Sulfate transporter protein	Foito *et al.* (2009)
Lotus sp.	Transcriptomics	↓ Proteins related to the synthesis of threonine, serine and glutamic acid	Sanchez *et al.* (2012)
Pinus radiata	Transcriptomics	Expression of 73 genes ♦ Expression of 43 genes	Heath *et al.* (2002)
Populus balsamifera	Transcriptomics	↑ Galactinol synthetase, stachyose synthetase	Hamanishi *et al.* (2010)
Pinus pinaster	Transcriptomics	↑ Glycolate oxidase synthesis	Dubos & Plomion (2003)
Pinus taeda	Transcriptomics	Variation in expression of 42 genes	Lorenz *et al.* (2005)
Pinus pinaster	Transcriptomics	↑ Expression of 28 genes ↓ Expression of 20 genes	Dubos *et al.* (2003)
Pinus taeda	Transcriptomics	↑ Expression of genes involved in cell-wall reinforcement	Chang *et al.* (1996)
Populus alba	Transcriptomics	↑ Expression of 199 genes (among them enzymes related to protein degradation) ↓ Expression of 253 genes (among them enzymes related to cellulose synthesis)	Berta *et al.* (2010)
Populus sp.	Transcriptomics	↑ Expression of genes linked to leaf abscission	Street *et al.* (2006)
Physcomitrella patents	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Cuming *et al.* (2007)
Lotus japonicus	Transcriptomics	↑ Expression of genes related to proline synthesis pathway	Díaz *et al.* (2010)
Lolium perenne	Transcriptomics	↑ Expression of genes related to glutathione peroxidase and superoxide dismutase synthesis pathways	Liu & Jiang (2010)
Hordeum vulgare	Transcriptomics	↑ Upregulation of the enzymes linked to ABA synthesis pathway	Seiler *et al.* (2011)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Arabidopsis thaliana	Transcriptomics	↑ Expression of genes related to control of stomatal openness	Aubert *et al.* (2010)
Populus sp.	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Cohen *et al.* (2010)
Nicotina tabacum	Transcriptomics	↑ Expression of genes related to proline and superoxide dismutase synthesis pathways	Li & Han (2012)
Festuca mairei	Transcriptomics	464 transcript fragments were differently expressed under drought ↓ Expression of genes related to transcription and DNA processing	Wang & Bughrara (2007)
Cleistogenes songorica	Transcriptomics	↑ Expression of 8 genes ↓ Expression of 5 genes	Zhang *et al.* (2011a)
Avena barbata	Transcriptomics	↓ Expression of genes related to N remobilization	Swarbreck *et al.* (2011)
Oriza sativa	Transcriptomics	↑ Expression of genes related to cell turgor	Rabello *et al.* (2008)
Populus balsamifera	Transcriptomics	↑ Expression of genes related to raffinose synthesis pathway	Hamanishi *et al.* (2010)
Populus nigra	Transcriptomics	↑ Expression of genes related to starch mobilization to produce soluble sugars	Regier *et al.* (2009)
Zea mays	Transcriptomics	↑ Expression of genes related to ABA synthesis pathway	Jiang *et al.* (2012)
Gossypium sp.	Transcriptomics	↑ Expression of genes related to cell-wall loosening and cell expansion	Padmalatha *et al.* (2012)
Quercus suber	Transcriptomics	↑ Expression of genes related to glucose, fructose, galactose, manitol and quercitol synthesis pathways	Spieb *et al.* (2012)
Populus nigra	Transcriptomics	↑ Expression of genes related to starch degradation pathways	Regier *et al.* (2009)
Avena barbata	Transcriptomics	↓ Expression of genes related to C and N metabolism	Swarbreck *et al.* (2011)
Medicago sativa	Transcriptomics	↑ Sucrose synthetase and nitrogenase	Naya *et al.* (2007)
Oryza sativa	Transcriptomics	↑ Synthesis of transcriptomic factor protein AP37	Oh *et al.* (2009)
Arabidopsis sp.	Transcriptomics	↑ Synthesis of protein LEW1 linked to dolichol biosynthesis pathway	Zhang *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ DREB2A expression	Perera *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Drought-inducible genes and discovery of DRIP1 and DRIP2 genes involved in DREBA protein proteolysis	Qin *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Discovery of OCP3 transcription factors that actuate a drought ABA-responsive mechanism	Ramírez *et al.* (2009)
Solanum tuberosum ssp. *andigena*	Transcriptomics	↑ Sucrose phosphatase and glucose pyrophosphatase transcription	Watkinson *et al.* (2008)
Triticum durum, *Aegilops kotschii*, *Aegilops umbellulata*	Transcriptomics	↑ Expression of 5 dehydrin genes	Rabello *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ DREB2A expression that stimulates the expression of drought-responsive genes	Sakuma *et al.* (2006)
Arabidopsis sp.	Transcriptomics	↑ Discovery of the gene encoding protein nucleotidase/phosphatase SAL1 that is a negative regulator of drought-tolerance genes	Wilson *et al.* (2009)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
Arabidopsis sp.	Transcriptomics	↑ Discovery of the gene encoding the factor HYB96 that is upregulated under drought and integrates ABA and auxin signals under drought	Seo *et al.* (2009)
Nicotina tabacum	Transcriptomics	↑ Receptor kinase protein was related and cytokinin-dependent photorespiration protein that increases plant resistance to drought	Rivero *et al.* (2009)
Thellungiella halophila	Transcriptomics	↑ Synthesis of vacuolar pyrophosphatase	Li *et al.* (2008a,b)
Zea mays	Transcriptomics	↑ 51 transcripts	Fernandes *et al.* (2008)
Cajanus cajan	Transcriptomics	↑ Expression of hybrid proline-rich protein	Priyanka *et al.* (2010)
Arabidopsis thaliana	Transcriptomics	Discovery of the gene related to the feedback mechanisms between responses to drought and changes in the circadian clock	Legnaioli *et al.* (2009)
Tabacum sp.	Transcriptomics	↑ Expression of phospholipases that increased drought resistance at short-term	Hong *et al.* (2008)
Arabidopsis sp., *Brassica napus*	Transcriptomics	↓ Expression of farnesyltransferase	Wang *et al.* (2009)
Oryza sativa	Transcriptomics	Discovery of the gene encoding mitogen-activated protein kinase that mediates in drought tolerance by scavenging reactive oxygen species	Ning *et al.* (2010)
Arabidopsis sp.	Transcriptomics	↑ Expression of two genes (PUB22 and PUB 23)	Cho *et al.* (2008)
Molecular responses of organisms to WARMING			
Saussurea alpina, *Tofieldia pusilla*, *Carex vaginata*, *Vaccinium ulginosum*, *Salaginella selaginoides*	HPLC-UV (target metabolomics)	No effects on plant secondary compounds	Nybakken *et al.* (2011)
Arabidopsis thaliana	Metabolomics (GC-MS)	↑ Several sugars, leucine, valine, tyrosine, uracil, quinic acid, xylitol	Kaplan *et al.* (2004)
Agrostis stolonifera	Metabolomics (GC-MS)	↑ Lipid unsaturation	Larkindale & Huang (2004)
Drosophila sp.	Metabolomics (^{1}H NMR)	↑ Leucine, valine, tyrosine	Malmendal *et al.*, 2006;
Belgica antarctica	Metabolomics (GC-MS)	↓ Serine	Michaud *et al.* (2008)
Schizosaccharomyces pombe	Metabolomics (LS-MS)	↑ Some amino acids, threhalose, glycerophosphoethanolamine, arabitol, ribulose, ophthalmic acid Many changes in secondary metabolites such as ↓ urea-cycle intermediates and ↑ acetylated compounds	Pluskal *et al.* (2010)
Erica multiflora	Metabolomics (^{1}H NMR)	↑ Fatty acids, compounds related to amino acid and sugar metabolism	Rivas-Ubach *et al.* (2012)
Arabidopsis sp.	Metabolomics (GC-MS)	↑ Sucrose, maltose, glucose	Rizhsky *et al.* (2004)
Oncorhynchus mykiss	Metabolomics (^{1}H NMR)	Different metabolomic fingerprinting	Turner *et al.* (2007)
Oncorhynchus mykiss	Metabolomics (^{1}H NMR)	↑ Metabolites related to antithermal stress protein pathways, ATP, glycogen	Viant *et al.* (2003)
Folsomia candida	Metabolomics (^{1}H NMR)	↓ Arginine, lysine, leucine, phenylalanine, tyrosine (after 7 hr heat exposure)	Waagner *et al.* (2010)
Oryza sativa	Metabolomics (Capillary electrophoresis-MS)	↑ Sucrose, pyruvate/oxaloacetate-derived amino acids ↓ Sugar phosphates and organic acids involved	Yamakawa & Hakata (2010)

Table 1 (continued)

Species	Analytical techniques used	Principal results	References
		in glycolysis/gluconeogenesis and the tricarboxylic acid cycle (TCA)	
Macrosiphum euphorbiae	Proteomics	↓ Proteins involved in energy metabolism	Nguyen *et al.* (2009)
Agrostis scabra, *Agrostis stolonifera*	Proteomics	↑ Proteins involved in photosynthesis and heat-shock proteins	Xu & Huang (2008a,b, 2010) and Xu *et al.* (2008)
Pinus armandii	Proteomics	8 proteins changed their concentrations under warming	He *et al.* (2007)
Triticum aesticum	Proteomics	↑ Some gluteninss proteins	Yang *et al.* (2011)
Festuca sp.	Transcriptomics	↑ Expression of genes related to transcription and photosynthesis	Zhang *et al.* (2005a)
Avena barbata	Transcriptomics	↑ Expression of genes related to N remobilization	Swarbreck *et al.* (2011)
Arabidopsis sp.	Transcriptomics	↑ Protein BOBBER1	Perez *et al.* (2009)
Arabidopsis sp.	Transcriptomics	↑ Expression of NFYAS5 transcription factor that is related to the transcription of stress-response genes	Li *et al.* (2008a,b)
Solanum tuberosum	Transcriptomics	↑ Genes related to cell proliferation, hormone synthesis and antistress mechanisms were upregulated	Ginzberg *et al.* (2009)
Boea hygrometrica	Transcriptomics	↑ Expression of BhHsf1 transcriptional factor that is related to thermotolerance	Zhu *et al.* (2009)
Zea mays	Transcriptomics	↑ 754 transcripts	Fernandes *et al.* (2008)
Arabidopsis sp.	Transcriptomics	↑ Expression of peptidyl prolyl cis/trans isomerase	Meiri & Breiman (2009)
Arabidopsis sp.	Transcriptomics	Epression of dehydration-response element binding protein (DREB2A)	Schramm *et al.* (2008)
Oryza sativa	Transcriptomics	↑ Expression of 23 genes related to heat-shock protein synthesis	Sarkar *et al.* (2009)
Chenopodium album	Transcriptomics	↑ Expression of heat-shock proteins	Barua *et al.* (2008)

2008b, 2010; Xu *et al.*, 2008). The experimental data currently available suggest that the response of plants to warming does not imply important changes in secondary compounds. For example, Nybakken *et al.* (2011) observed that warming had little effect on the concentrations of carbon-based secondary compounds in subalpine ecosystems.

The individual molecular responses of plants to drought and warming are frequently related to physiological (Xu & Zhou, 2006; He *et al.*, 2008; Aubert *et al.*, 2010; Yang *et al.*, 2010; Aranjuelo *et al.*, 2011), phenological (Swarbreck *et al.*, 2011) and anatomical (Spieb *et al.*, 2012) responses. Moreover, changes in the molecular composition of plants in response to drought are linked to changes in elemental stoichiometry (Rivas-Ubach *et al.*, 2012) (Fig. 2), with different levels of response among the species of the same community (Peñuelas *et al.*, 2008a). Changes in plant C : N : P stoichiometry affect the cycling of nutrients in ecosystems, the transfer of energy throughout trophic webs and the composition of herbivore communities (Elser *et al.*, 2000, 2009; Elser, 2006; Sardans *et al.*, 2012a). All these shifts in the chemical composition of plants can thus have further consequences on the functioning of trophic webs (Peñuelas & Sardans, 2009), which warrants future research based mainly on long-term observations and experiments.

Studies on the molecular impacts of drought and warming on wild terrestrial animals are less common. Nguyen *et al.* (2009) observed that individual aphids exposed to elevated temperatures presented lower growth, lower abundances of several enzymes of central pathways of energy metabolism and increased production of exoskeletal proteins. Metabolomic studies in insects further confirmed that heat stress increases the levels of some amino acids and proteins and decreases the metabolism of sugar (Malmendal *et al.*, 2006; Michaud *et al.*, 2008) (Table 1).

This overview of current bibliography of omic studies of the impacts of climate change shows that these techniques have a high sensitivity to detect metabolome shifts of organisms submitted to drought and/or warming. They show a fast increase in the synthesis of enzymes, metabolic pathways and metabolites linked

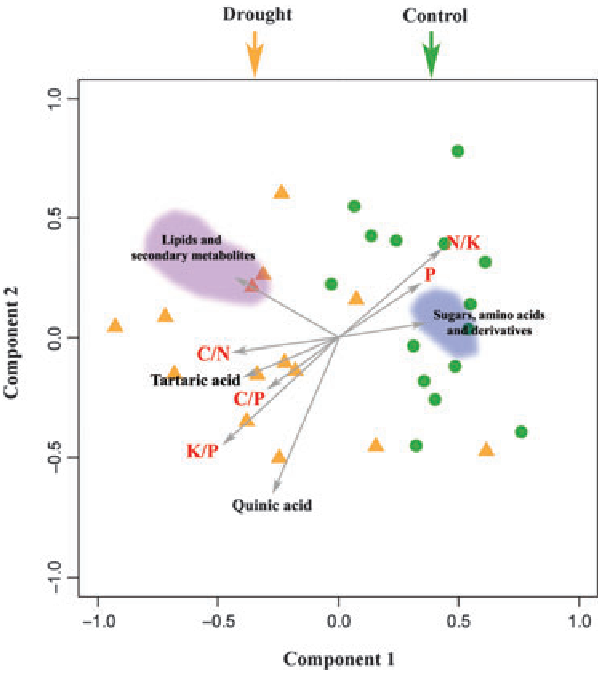

Fig. 2 PLS-DA analysis of the stoichiometry and metabolomics of leaves of *Erica multiflora* shrubs submitted to the effects of a moderate experimental field drought (Based on Rivas-Ubach *et al.*, 2012). (triangles: drought; circles: control).

to osmotic control and antistress mechanisms. However, there is a lack of studies coupling climatic change and genomics-metabolomics with nutrient cycles, availability and stoichiometry, with physiological and phenological changes and with shifts in ecosystem structure. These integrated studies should provide a better understanding of the mechanisms and processes underlying the change in resource use, in intraspecies and interspecies competition and in species substitution and selection under global change.

Physiological and morphological

An organism's capacity for physiological adaptation is a key factor in its success in adapting to climate change (Bernardo *et al.*, 2007). A plant's response to drought includes several physiological responses. There are changes in the allocation of resources, decreases in net photosynthetic rate, decreases in efficiency of carboxylation, increases in the efficiency of PSII photochemistry and increases in water use efficiency (WUE) that frequently accompany a decrease in plant growth and reproductive output, the intensities of which differ among communities and species (Table 2). The shifts in enzymatic machinery necessary for these changes are linked to shifts in N metabolism, consisting of a decrease in the activity of key enzymes related to N anabolism, such as nitrate reductase and glutamine synthase, and an increase in enzymatic activity related to N catabolism and transport, such as the activity of asparaginase (Xu & Zhou, 2006). As reported in the previous section, a shift of protein content occurs under drought from proteins related to photosynthesis and carboxylation to proteins linked to antistress systems (Table 1). Fine-scale studies using ^{1}H nuclear magnetic resonance (NMR) imaging have observed that leaves of the Mediterranean tree *Quercus ilex* under prolonged drought are able to maintain water in parenchymal tissues for a longer time than in vascular tissues, which allows the most active parts of the leaves to be more hydrated for a longer time (Sardans *et al.*, 2010). These conservative mechanisms are frequently able to minimize the negative effects of drought on plant growth (Molina-Montenegro *et al.*, 2011; Peñuelas *et al.*, 2011a, b). These mechanisms also have negative impacts, however, such as a decrease in nutrient uptake resulting from the decrease in plant transpiration (Peñuelas *et al.*, 1993; Cramer & Hawkins Verboom, 2009; Cernusak *et al.*, 2011) or a decrease in the production of root phosphatases (Sardans *et al.*, 2007). Plants can compensate for this low uptake of nutrients by enhancing their reabsorption of nutrients (Heckathorn & DeLucia, 1994; Devakumar *et al.*, 1999; Marchin *et al.*, 2010). This increased reabsorption, together with a higher synthesis of C-rich secondary compounds under drought (Hale *et al.*, 2005), decrease the quality of leaf litter, which has a negative feedback effect on productivity by decreasing, decomposition rates of soil organic matter and the availability of nutrients (Yaire & van Cleve, 1996; Sardans & Peñuelas, 2004, 2005).

An organism's response to warming depends on whether or not the ecosystem is limited by water and on whether or not the climate is cold (Table 2). In ecosystems not limited by water, the photosynthetic capacity of plants and, in general, the changes in plant function under warming strongly depends on the capacity of each species to adapt its optimal temperature of maximal rates of assimilation (Gunderson *et al.*, 2010; Sardans & Peñuelas, 2010; Zelikova *et al.*, 2012). Plants generally tend to increase their optimal photosynthetic temperatures under warming, which differ among species (Gunderson *et al.*, 2010). This photosynthetic acclimation can increase plant production capacity if other resources such as nutrients are not limiting. In this way, the capacity of a plant to invest in mechanisms for enhancing the availability and uptake of nutrients is critical for enhancing growth (Michelsen *et al.*, 1996; Henry & Molau, 1997; Jónsdóttir *et al.*, 2005b). Plants under warming can respond by increasing N_2 fixation (Sorensen & Michelsen, 2011), mycorrhizal intensity (Rillig *et al.*, 2002; Staddon *et al.*, 2004; Olsrud *et al.*, 2010; Yergeau *et al.*, 2012), root enzymes

Table 2 Main results of available studies on the effects of drought and warming on growth, production (photosynthesis), reproductive capacity or resources use and allocation

Biome and species	Study type	Main results	Reference
Effects of drought			
Tropical forest (Gen *Shorea*, Gen *Dacrydium*, Gen *Payena*)	Field observation	↓ Growth in some species and no effects on growth in other species	Aiba & Kitayama (2002)
Temperate shrubland (*Calluna vulgaris*)	Field climate manipulation	↓ Photosynthetic activity	Albert *et al.* (2011a)
Temperate grassland (*Deschampsia flexuosa*)	Field climate manipulation	↓ Growth	Albert *et al.* (2011b)
Temperate grassland (*Alopecurus pratensis*, *Arrhenaterum elatius*, *Festuca pratensis*, *Holcus lanatus*)	Common garden	↓ Growth, but with different intensities depending on species	Belerkuhnlein *et al.* (2011)
Boreal forest (*Picea* sp.)	Common garden	↓ Photosynthetic activity	Bigras (2005)
Temperate grassland (*Festuca arundinacea*, *Poa pratensis*, *Festuca rubra*, *Agrostis capillaries*, *Stellaria graminea*, *Veronica chamaedrys*, *Vicia sativa*)	Field climate manipulation	↓ Growth	Bloor *et al.* (2010)
Mediterranean forest (*Pinus halepensis*)	Field climate manipulation	↓ Growth	Borghetti *et al.* (1998)
13 conifer species	Greenhouse	↑ WUE	Brodribb & Hill (1998)
Temperate forest (*Pinus ponderosa*)	Field gradient study	↓ Allocation of C to leaves	Callaway *et al.* (1994)
Temperate grassland (*Lotus corniculatus*)	Greenhouse	↑ Aboveground growth and reproductive output ↓ Belowground growth	Carter *et al.* (1997)
Semiarid grassland (*Cryptantha flava*)	Field climate manipulation	↓ Growth	Casper *et al.* (2006)
Mediterranean grassland (*Setaria parviflora*)	Field climate manipulation	↓ Growth	Chuine *et al.* (2012)
Mediterranean forest (*Quercus ilex*)	Field observation	↓ Growth	Corcuera *et al.* (2004)
Temperate forest (*Pinus ponderosa*)	Field observation	↓ Growth	Fernandez *et al.* (2012)
Vitis vinifera	Field climate manipulation	↓ Photosynthetic activity	Flexas *et al.* (2004)
Temperate grassland (*Hypericum perforatum*)	Field climate manipulation	↓ Growth and reproductive output	Fox *et al.* (1999)
Temperate and alpine grasslands	Field observation	↓ Belowground growth and inconclusive results on aboveground growth	Frank (2007)
Temperate shrubland (*Calluna vulgaris*, *Pteridium aquilinum*)	Common garden	↓ Growth	Gordon *et al.* (1999a,b)
Temperate forest (*Populus nigra*)	Greenhouse	↓ Growth and photosynthetic activity	Hale *et al.* (2005)
Temperate forest (*Acer rubrum*, *Acer saccharum*, *Betul papyrifera*, *Betula alleghamiensi*)	Field observation	↓ Growth, but with different intensities depending on the species	He *et al.* (2005)
Temperate grassland (*Dactylis glomarata*, *Elymus repens*, *Phleum pratense*, *Poa* sp., *Setaria glauca*, *Setaria viridis*, *Plantago lanceolata*, *Taraxacum officinalis*, *Potentilla argentea*, *Silene latifolia*, *Achillea millefolium*, *Tanacetum vulgare*)	Field climate manipulation	↓ Reproductive output	Hoeppner & Dukes (2012)
Pinus halepensis	Pot experiment	↓ Growth	Inclan *et al.* (2005)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Boreal forest (*Picea abies*)	Field climate manipulation	↓ Growth	Jyske *et al.* (2010)
Alpine forest (*Abies alba*)	Field observation	↓ Growth	Liancourt *et al.* (2012)
Mediterranean shrubland (*Erica multiflora, Globularia alypum*)	Field climate manipulation	↓ Photosynthetic activity	Llorens *et al.* (2003)
Mediterranean shrubland (*Erica multiflora, Globularia alypum*)	Field climate manipulation	↓ Growth	Alla *et al.* (2012), Lloret *et al.* (2004a,b), Loe *et al.* (2005)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↑ WUE	Lloret *et al.* (2004a,b)
Temperate forest (*Fagus sylvatica*)	Field observation	↓ Belowground growth	Meier & Leuschner (2008)
Mediterranean forest (*Pinus halepensis*)	Field observation	↓ Growth	Moreno-Gutiérrez *et al.* (2012)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↑ WUE	Ogaya & Peñuelas (2003)
Mediterranean forest (*Arbutus unedo, Phillyrea latifolia, Quercus ilex*)	Field climate manipulation	↓ Growth of *A. unedo* and *Q. ilex* No effects on *P. latifolia*	Ogaya & Peñuelas (2007a,b)
Rainforest	Review of field observational studies	↓ Growth and photosynthetic activity	Parolin *et al.* (2010)
Mediterranean forest (*Quercus ilex*)	Field climate manipulation	Changes in N allocation to leaves depending on drought intensity	Peña-Rojas *et al.* (2006)
Temperate and Mediterranean shrublands	Field climate manipulation	↓ Growth of Mediterranean shrublands and no effects on growth of temperate shrublands	Peñuelas *et al.* (2004a)
Mediterranean forest (*Phillyrea latifolia, Quercus ilex*)	Field observation	↑ WUE	Peñuelas *et al.* (2000a)
Mediterranean, semiarid and tropical biomes	Metadata analysis	↑ WUE	Peñuelas *et al.* (2011a,b)
Mediterranean forest (*Quercus ilex*)	Field climate manipulation	↓ Reproductive output	Pérez-Ramos *et al.* (2010)
Temperate forest (*Fagus sylvatica,*)	Pot experiment	↓ P allocation to leaves	Peuke & Rennenberg (2004)
Temperate forest (*Fagus sylvatica, Picea abies*)	Field observation	↓ Growth	Pretzsch & Dieler (2011)
Temperate shrublands (*Erica multiflora, Globularia, Pinus halepensis*)	Field climate manipulation	Different effects on photosynthetic activity depending on species and season	Prieto *et al.* (2009a)
Temperate shrublands (*Erica multiflora, Globularia, Pinus halepensis*)	Field climate manipulation	↓ Growth	Prieto *et al.* (2009b)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Temperate grassland (*Brassica napus*)	Common garden	↓ Growth	Qaderi *et al.* (2006)
Temperate forest	Review of field observational and experimental studies	↓ Photosynthetic activity	Rennenberg *et al.* (2006)
Temperate grassland (*Leymus chinensis*)	Field observation	↓ Growth and reproductive output	Renzhong & Qiong (2003)
Semiarid shrubland (*Larrea tridentate*, *Propopsis glandulosa*)	Field climate manipulation	No conclusive results regarding growth	Reynolds *et al.* (1999)
(*Alloteropsis semialata*, *Panicum aequinerve*, *Tristacya leucothrix*, *Themeda triandra*)	Pot experiment	↓ Photosynthetic activity	Ripley *et al.* (2010)
Mediterranean shrubland (*Globularia alypum*, *Erica multiflora*, *Dorycnium pentaphyllum*)	Field climate manipulation	↓ Allocation to leaves	Sardans *et al.* (2008a)
Continental shrubland (*Oryzopsis hymenoides*, *Gutierrezia sarothrae*, *Ceratoides lantana*)	Field climate manipulation	↓ Growth	Schwinning *et al.* (2005)
Mediterranean forest (*Quercus ilex*, *Phillyrea latifolia*)	Field climate manipulation	↓ Photosynthetic activity	Serrano & Peñuelas (2005)
Temperate grassland (*Phleum pratense*, *Trifolium repens*, *Rumex obtusifolium*)	Field climate manipulation	↓ Photosynthetic efficiency	Signarbieux & Feller (2011)
Temperate forest (*Pinus nigra*)	Common garden	No effects on growth	Thiel *et al.* (2012)
Temperate forest (*Quercus stellata*, *Junniperus virginiana*, *Schizachyrium scoparium*)	Field climate manipulation	↓ Photosynthetic activity	Volder *et al.* (2010)
Alpine forest (*Picea crassifolia*)	Field observation	↓ Growth	Wang *et al.* (2012)
Temperate forest (*Pinus taeda*)	Field climate manipulation	↓ Growth and photosynthetic activity	Wertin *et al.* (2012)
Mediterranean shrubland (*Leucadedron* sp., *Erica* sp., *Diastella divaricata*)	Field climate manipulation	↓ Growth of anisohydric species, isohydric species were unaffected	West *et al.* (2012)
Tropical grassland (*Pennisetum setaceum*, *Heteropogon contortus*)	Greenhouse	↓ Growth	Williams & Black (1994)
All biome types	Meta-analysis of 85 sites with field climate manipulation	↓ Growth	Wu *et al.* (2011a,b)
Temperate grassland (*Leymus chinensis*)	Field climate manipulation	↓ Photosynthetic activity	Xu & Zhou (2006)
Effects of warming			
Temperate shrubland (*Calluna vulgaris*)	Field climate manipulation	↑ Photosynthetic activity	Albert *et al.* (2011a)
Temperate grassland (*Deschampsia flexuosa*)	Field climate manipulation	↑ Growth	Albert *et al.* (2011b)
Tundra (13 different sites)	Field climate manipulation	↑ Growth in lower tundra and ↑ Growth in low tundra and	Arft *et al.* (1999)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
		↑ Reproductive output in high tundra sites	
Tundra (*Vaccinium sp.*, *Betula nana*, *Carex eusifolia*, lichen species)	Field climate manipulation	↑ Increase in growth of most species	Biasi *et al.* (2008)
Boreal forest (*Picea mariana*)	Field climate manipulation	↑ Growth	Bronson *et al.* (2009)
Tundra	Field climate manipulation	↑ Growth in shrub species ↓ Growth of nonvascular plants	Chapin *et al.* (1995)
Tundra (*Ceratodon purpureus*, *Bryum pseudotriquetrum*, *Bryoerythrophyllum recurvirostre*)	Field observation	↑ Growth, effect related to an increase in water availability	Clarke & Zani (2012)
Alpine shrubland (*Vaccinium myrtilus*, *Vaccinium gautheroides*, *Empetrum hermaphroditum*)	Field climate manipulation	↑ Growth of *V. myrtilus* and no effects on *V. gautheroides* and *E. hermaphroditum*	Dawes *et al.* (2011)
Tundra (*Deschampsia Antarctica*, *Colobanthus quitensis*)	Field climate manipulation	↑ Reproductive output	Day *et al.* (1999)
Temperate grassland (*Dactylis glomerata*, *Festuca arundinacea*, *Lolium perenne*, *Trifoliun repens*, *Medicago sativa*, *Plantago lanceolata*, *Bellis perennis*, *Rumex acetosa*)	Common garden	↓ Growth related to higher evapotranspiration and lower soil moisture	De Boeck *et al.* (2007, 2008)
Grassland of temperate forest understory (*Anemone nemorosa*, *Milium effusum*)	Field climate manipulation	↑ Growth and reproductive output	De Frenne *et al.* (2011)
Boreal peatland (*Sphagnum fuscum*)	Field climate manipulation	↑ Growth	Dorrepaal *et al.* (2003)
Alpine grassland	Field climate manipulation	↑ Belowground growth	Egli *et al.* (2004)
Tundra (46 different sites)	Field observation	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Elmendorf *et al.* (2012a)
Tundra (61 different sites)	Field climate manipulation	↑ Growth of shrubs in warmer sites and of herbs in colder sites	Elmendorf *et al.* (2012b)
Alpine grassland (*Poa alpina*, *Artemisia ginepi*, *Trifolium pallescens*, *Anthyllis vulneraria*)	Field climate manipulation	↑ Growth	Endels *et al.* (2007)
Tropical forest (*Cedrela odorata*, *Cliricidia sepium*)	Greenhouse	↑ Growth	Esmail & Oelbermann (2011)
Temperate forest	Field climate manipulation	↑ Growth of trees and shrubs but not herbs	Farnsworth *et al.* (1995)
Temperate grassland (*Andropogon gerardii*, *Sorghastrum mutans*, *Panicum*	Field climate manipulation	↓ Productivity in summer	Fay *et al.* (2011)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
virgatum, *Sporobolus asper*, *Solidago canadensis*, *Aster ericoides*, *Solidago missouriensis*)			
Temperate grassland (*Leymus chinensis*)	Field observation	↑ Reproductive output	Gao *et al.* (2012)
Temperate shrubland (*Calluna vulgaris*, *Pteridium aquilinum*)	Common garden	↑ Growth of *C. vulgaris*, and no effects on the growth of *P. aquilinum*	Gordon *et al.* (1999a,b)
Temperate grassland (*Juncus gerardii*, *Spartina patens*, *Spartina alterniflora*, *Plantago maritima*, *Analgis maritima*, *Atriplex patula*, *Glaux maritima*, *Suaeda maritima*)	Field climate manipulation	↑ Growth of *Plantago maritima* and ↓ growth of *Juncus gerardii*, *Spartina patens*	Gedan & Bertness (2009)
Temperate forest (*Liquidambar atyraciflua*, *Quercus rubra*, *Quercus falcate*, *Betula alleghaniensis*, *Populus grandidentata*)	Field climate manipulation	↑ Increases in the optimal temperature for maximal photosynthetic activity	Green (2010)
Subarctic shrubland (*Empetrum hemaphroditum*, *Vaccinum myrtilus*, *Vaccinum ulginosum*, *Vaccinum vitis-idaea*)	Field climate manipulation	↑ Growth	Hartley *et al.* (1999)
Subtropical grassland (*Eupatorium adenophorum*, *Eupatorium chinense*)	Pot experiment	↑ Growth, but more in the invasive species, *E. adenophorum*	He *et al.* (2012)
Tundra	Review of 26 field climate-manipulation experiments	↑ Growth depending on nutrient availability	Henry & Molau (1997)
Tundra (*Carex* sp.)	Field observational	↑ Growth	Hill & Henry (2011)
Tundra (several vascular and nonvascular plants)	Field climate manipulation	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Hobbie *et al.* (1999)
Temperate grassland (*Dactylis glomerata*, *Elymus repens*, *Phleum pratense*, *Poa sp.*, *Setaria glauca*, *Setaria viridis*, *Plantago lanceolata*, *Taraxacum officinale*, *Achillea millefolium*, *Potentilla argentea*, *Silene latifolia*, *Tanacetum vulgare*)	Field climate manipulation	No conclusive results regarding growth	Hoeppner & Dukes (2012)
Tundra (*Betula* sp.)	Field climate manipulation	No conclusive results regarding growth	Hofgaard *et al.* (2010)
Tundra (*Carex aquatilis*, *Salix rotundifolia* and several herb species)	Field climate manipulation	↑ Growth of herbs but not of the entire community	Hollister & Flaherty (2010)
Tundra	Field climate manipulation in 4 sites	↑ Growth of vascular plants and ↓ growth of nonvascular plants	Hollister *et al.* (2005)
Tundra	Field climate manipulation	↑ Growth of grasses but not of the entire community	Hollister & Flaherty (2010)
Temperate grassland (Several C3 and C4 grasses)	Field climate manipulation		Hovenden *et al.* (2007)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
		↑ Reproductive output in perennial grasses but no effects in the other grass groups	
Temperate grassland (*Poa pratensis*, *Bromus mermis*, *Cirsium arvense*, *Lotus corniculatus*)	Field climate manipulation	↑ Growth	Hutchison & Henry (2010)
Alpine grassland (*Asterolasia trymalioides*, *Carex sp.*, *Celmsia pugioniformis*, *Plantago euryphylla*, *Poa hiemata*, *Pimela alpine*)	Field climate manipulation	↑ Growth	Jarrad *et al.* (2009)
Tundra (*Carex bigelowii*)	Field climate manipulation	↑ Growth	Jónsdóttir *et al.* (2005a)
Tundra (Diverse vascular and nonvascular plants)	Field climate manipulation	↑ Growth of vascular plants and ↓ growth of nonvascular plants but greater effects in nutrient-rich sites	Jónsdóttir *et al.* (2005b)
Temperate shrubland (*Calluna vulgaris*, *Deschampsia flexuosa*)	Field climate manipulation	No effects on growth	Kongstad *et al.* (2012)
Temperate grassland and shrublands	Common garden experiment	↑ Growth in grasses and ↓ growth in shrubs	Kreyling *et al.* (2011)
Temperate shrublands (*Ledum palustre*, *Empetrum nigrum*, *Vaccinium uliginosum*, *Arctous alpinus*, *Vaccinium vitis vinifera*)	Field climate manipulation	↑ Growth of evergreen shrubs and no effects on deciduous shrubs	Kudo & Suzuki (2003)
Alpine grassland (*Delphinium nuttallianum*, *Helianthella quinquenervia*, *Erythronium grandiflorum*, *Erigeron speciosus*)	Field climate manipulation	↑ Reproductive output of *D. nuttallianum* and *H. quinquinervia* and no effects in the other two species	Lambrecht *et al.* (2006)
Alpine grassland (diverse *Korbresia specis*, *Carex scabriopsis*, *Carex atrofusca*)	Field climate manipulation	↑ Growth	Li *et al.* (2011a)
Alpine grassland (*Potentilla anserina*, *Elymus nutants*, *Kobresias* species, *Anemone trullifolia*)	Field climate manipulation	↓ Growth due to ↑ of herbivorous activity	Li *et al.* (2011b)
Continental grassland (*Carex pediformis*, *Festuca lenensis*, *Koeleria macrantha*, *Helictotrichon*, *Aster alpinus*, *Potentilla acaulis*, *Artemisia commutata*)	Field climate manipulation	↓ Reproductive output	Liancourt *et al.* (2012)
Alpine grassland (*Deschampsia caespitosa*, *Anemone trullifolia*, *Potentilla anserine*, *Haplasphaera*, *Aster alpines*, *Gentiana formosa*, *Blymus sinocompressus*)	Field climate manipulation	↓ Reproductive output	Liu *et al.* (2012)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*)	Field climate manipulation	↑ Photosynthetic activity in cold periods	Llorens *et al.* (2003)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*)	Field climate manipulation	↑ Growth of *E. multiflora* and ↓ growth of *G. alypum*	Alla *et al.* (2012), Lloret *et al.* (2004a,b), Loe *et al.* (2005)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Boreal forest (*Picea abies*, *Populus tremuloides*)	Field observation	↑ Growth	Messaoud & Chen (2011)
Tundra (*Cassiope tetragona*, *Empetrum hermaphroditium*)	Field climate manipulation	↑ Growth	Michelsen *et al.* (1996)
Tundra (*Cassiope tetragona*, *Rannunculus nivalis*)	Field climate manipulation	↑ Reproductive output	Molau (1997)
Tundra (Papaver radicatum)	Field climate manipulation	↑ Growth	Molgaard & Christensen (1997)
Alpine grassland (*Cassia* and *Kobresia* species)	Field climate manipulation	↑ Growth	Na *et al.* (2011)
Tundra (*Eriophorum vaginatum*, *Carex bigelowii*, *Betula nana*, *Vaccinium ulginosum*, *Rubus chamamorus*, *Vaccinium vitis-idea*)	Field climate manipulation	↑ Growth	Natali *et al.* (2012)
Temperate grassland (*Lolium perenne*)	Field climate manipulation	↑ Growth	Nijs *et al.* (1996)
Temperate shrublands	Field climate manipulation	↑ Growth	Peñuelas *et al.* (2004a)
Temperate forest	Field observation	No significant growth changes	Peñuelas *et al.* (2008a,b)
Boreal, temperate and tropical forest	Field observation	No significant growth changes	Peñuelas *et al.* (2011a,b)
Alpine grassland (*Campanula rotundifolia*, *Acantium columbianum*, *Potentilla gracilis*, *Eriogonum subalpinum*, *Erigeron speciosus*)	Field climate manipulation	No significant growth changes related to decrease of soil moisture under warming	Price & Waser (2000)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*, *Pinus halepensis*)	Field climate manipulation	↑ Growth in *E. multiflora* and no effects in the other two species	Prieto *et al.* (2009a)
Mediterranean shrubland (*Erica multiflora*, *Globularia alypum*, *Pinus halepensis*)	Field climate manipulation	↑ Photosynthetic activity	Prieto *et al.* (2009b)
Mediterranean and temperate shrublands	Field climate manipulation	↑ Growth	Prieto *et al.* (2009c)
Tundra, grasslands and forest	Review (meta-analysis) of 32 studies of field climate manipulation	↑ Growth	Rustad *et al.* (2001)
Tundra	Field climate manipulation	No effects on growth	Shaver & Jonasson (1999)
Mediterranean grassland	Field climate manipulation	↑ Growth	Shaw *et al.* (2002)
Alpine grassland (*Elymus nutants*, *Potantilla anserine*)	Field climate manipulation	↑ Growth of *E. nutants* and ↓ growth of *P. anserine*	Shi *et al.* (2010)
Tropical grassland (*Wedelia trilobata*, *Widelia chinensis*)	Field climate manipulation	↑ Growth	Song *et al.* (2010)
Tundra	Field climate manipulation	↑ Photosynthetic activity	Starr *et al.* (2008)
Alpine grassland (*Saxifraga oppositifolia*)	Field climate manipulation	No conclusive results on reproductive output	Stenstrom *et al.* (1997)
Temperate grassland (*Bromus sterilis*, *Chenopodium album*, *Senecio vulgaris*, *Bellis perennis*)	Greenhouse	↑ Growth	Stirling *et al.* (1998)
Nezara viridula	Lab experiment	↑ Reproductive output	Takeda *et al.* (2010)
Temperate forest (*Pinus nigra*)	Common garden	No effect on growth	Thiel *et al.* (2012)
Temperate grassland (*Lathyrus latifolius*, *Cerastium tomentosum*, *Artemisa verlotiorum*)	Common garden	↑ Growth	Verlinden & Nijs (2010)

Table 2 (continued)

Biome and species	Study type	Main results	Reference
Subtropical grassland (*Phalaris aquatic*)	Field climate manipulation	No conclusive results on growth	Volder *et al.* (2004)
Alpine shrubland and grass-shrublands (*Empetrum nigrum*, *Loiseleuria procumbens*)	Field climate manipulation	↑ Growth of shrublands and no effects or ↓ growth in shrub-grasslands	Wada *et al.* (2002)
Tundra (*Betula nana*, *Eriophorum vaginatum*, *Salix pulchra*, *Sphagnum species*, *Vaccinium species*, *Ledum decumbens*)	Field climate manipulation	↑ Growth in shrubs and ↓ growth in grasses	Wahren *et al.* (2005)
Tundra	Review of 11 field climate-manipulation experiments	↑ Growth of vascular plants and growth of nonvascular plants	Walker *et al.* (2006)
Temperate grassland (*Artemisa frigid*, *Potentilla acaulis*, *Cleistogenes squarrosa*, *Allium bidentatum*, *Agropyron cristatum*)	Field climate manipulation	↑ Photosynthetic activity	Wan *et al.* (2009)
Temperate forest (*Acer rubrum*, *Acer saccharum*)	Field climate manipulation	↑ Growth production	Wan *et al.* (2004)
Temperate grassland	Field climate manipulation	↑ Growth in spring and autumn and ↓ growth in summer	Wan *et al.* (2005)
Boreal peatland (*Andromeda glaucophylla*, *Kalmia polifolia*)	Field climate manipulation	↑ Growth of shrubs and ↓ growth of grasses	Weltzin *et al.* (2003)
Temperate grassland (*Austrodanthonia caespitosa*, *Hypochaeris radicata*, *Leontodon taraxacoides*, *Themeda triandra*)	Field climate manipulation	↑ Growth of *A caespitose* and ↓ growth of *H. radicata* and *L. taraxacoides*	Williams *et al.* (2007)
All biome types	Meta-analysis of 85 sites with field climate manipulation	↑ Growth when not accompanied by a reduction in water availability	Wu *et al.* (2011a,b)
Temperate grassland	Greenhouse experiment	↑ Growth at short-term, but this response decreased progressively	Wu *et al.* (2012)
Semiarid grassland (*Artemisa frigida*, *Stipa ktylovii*, *Potentilla acaulis*, *Allium bidentatum*)	Field climate manipulation	No conclusive results on growth	Xia *et al.* (2009)
Alpine shrubland (*Cornicera hispida*, *Daphne refusa*)	Field climate manipulation	↑ Growth, no effects on reproductive output	Xu *et al.* (2009)
Alpine forest (*Abies faxoniona*, *Picea asperata*)	Field climate manipulation	↑ Growth and reproductive output	Yin *et al.* (2008)
Temperate grassland (*Ambrosia psilostachya*, *Helianthus mollis*, *Sorghastrum nutants*)	Field climate manipulation	↑ Photosynthesis in spring and ↓ photosynthesis in autumn	Zhou *et al.* (2007)

activity (Estiarte *et al*., 2008a) and turnover of fine roots (Wan *et al*., 2004). Most studies conducted in ecosystems not limited by water have thus observed increases in growth, photosynthetic activity and reproductive output of plants (Table 2). In tundra ecosystems limited by low temperatures, warming usually increases vascular plant growth and reduces nonvascular plant growth (Table 2), effects related to the increase in the availability of water (Clarke *et al*., 2012) and frequently limited by the availability of nutrients (Henry & Molau, 1997).

In contrast, plants under warming in dry areas respond to increased water deficits induced by associated increased evapotranspiration mainly by increasing their WUE (Brodribb & Hill, 1998; Peñuelas *et al*., 2008b) and generally by conservative mechanisms such as better control of photosynthetic capacity (Ogaya *et al*., 2011) and reduced growth (Table 2). A reduction in the availability of water has a negative effect on rubisco activity that limits CO_2 uptake (Flexas *et al*., 2004; Rennenberg *et al*., 2006). The physiological responses of plants to warming, therefore, range from changes that tend to increase plant production in cold-wet ecosystems to conservative responses that tend to increase the efficiency of use of resources in hot-dry ecosystems.

To complement these functional changes, plants can also alter their morphological structure to adapt to drought, mainly by increasing the allocation of carbon to the root system, thereby decreasing their stem/root ratio (Williams & Black, 1994; Xu *et al*., 2007; Meier & Leuschner, 2008; Shao *et al*., 2008; Dreesen *et al*., 2012), reducing their leaf size, increasing their leaf mass area (Ogaya & Peñuelas, 2006; Shao *et al*., 2008) and decreasing their leaf area index (Asner *et al*., 2004). The higher allocation of carbon to belowground tissues does not necessarily translate into a larger investment in mycorrhizal formation. Some studies have observed a trend of increasing investment in mycorrhizae (Shi *et al*., 2002), whereas others have observed the opposite trend (Staddon *et al*., 2004). The investment in mycorrhizal association under moderate drought can increase, but physiological stress limits the symbiosis at certain levels of drought (Shi *et al*., 2002).

Animals, particularly ectotherms, have several ways of physiologically adapting to warming. The most general and immediate responses in insects are an increase in metabolism and respiration (Neven, 2000) and the production of heat-shock proteins (Feder *et al*., 1997). When temperatures exceed a certain 'thermal limit', however, the number and intensity of the impacts on insect function threaten survival (Neven & Rehfield, 1995; Neven, 2000). Animals adapted to broad climatic gradients also have broad thermal tolerances and therefore respond better to the impacts of warming (Bonebrake & Deutsch, 2012). Moreover, spatial heterogeneity may play a critical role in thermal adaptation, particularly in the tropics where individuals can move to cooler or wetter parts of their current home ranges (Bonebrake & Deutsch, 2012) rather than altering their geographical distribution at the regional scale.

Growth and reproduction

Despite the observed phenotypic plasticity of plants in response to drought, a decrease in net production (Table 2) and reproduction (Ogaya & Peñuelas, 2007b) are the general responses of plants to drought. The intensities of these effects frequently differ among the species of a community (Peñuelas *et al*., 2004a; Ogaya & Peñuelas, 2007a,b; Wu *et al*., 2011a,b) and among the different levels of soil-water availability. A shift in phenology is one of the most conspicuous responses of plants and animals to current climate change (Körner, 1995; Peñuelas & Filella, 2001; Fitter & Fitter, 2002; Peñuelas *et al*., 2002, 2009b; Chuine *et al*., 2010) (Fig. 3). Climate warming has changed the life cycles of plants and animals, advancing the biological spring and delaying the arrival of biological autumn and winter (Peñuelas *et al*., 2002, 2009b; Badeck *et al*., 2004; Menzel *et al*., 2006; Steltzer & Post, 2009; Fridley, 2012). Several studies have observed significant advances in the timing of leaf expansion and flowering under warming in cold (Price & Waser, 1998; Thórhallsdóttir, 1998; Menzel & Fabian, 1999; Huelber *et al*., 2006), temperate (Peñuelas & Filella, 2001; Sherry *et al*., 2007; Rollinson & Kaye, 2012) and Mediterranean regions (Peñuelas & Filella, 2001; Peñuelas *et al*., 2002; Llorens & Peñuelas, 2005). In a meta-analysis of 125 000 observational series of 542 plant and 19 animal species in Europe, Menzel *et al*. (2006) observed that leaf unfolding had advanced 2.5 days per 1 °C of temperature increase, and leaf fall was delayed 1 day per 1 °C of temperature increase. Parmesan & Yohe (2003), in a review of available global data, reported an advance in leaf unfolding of 2.3 days per decade. These observations of advances in spring phases have been confirmed experimentally in the field in response to warming treatments of only about 1 °C (Llorens & Peñuelas, 2005; Prieto *et al*., 2009d). In most cases, though, the advances in these field experiments have been much lower than those observed in the field in recent decades (Wolkovich *et al*., 2012).

These effects, as those discussed earlier, vary for the different species of the community. For example, trees in temperate forests advance their leaf emergence to overlap with the period of emergence of the understory vegetation, thereby increasing competition (Rollinson & Kaye, 2012). Warming tends to advance flowering and fruiting in species that flower before the summer peak and delay flowering in species that flower after the

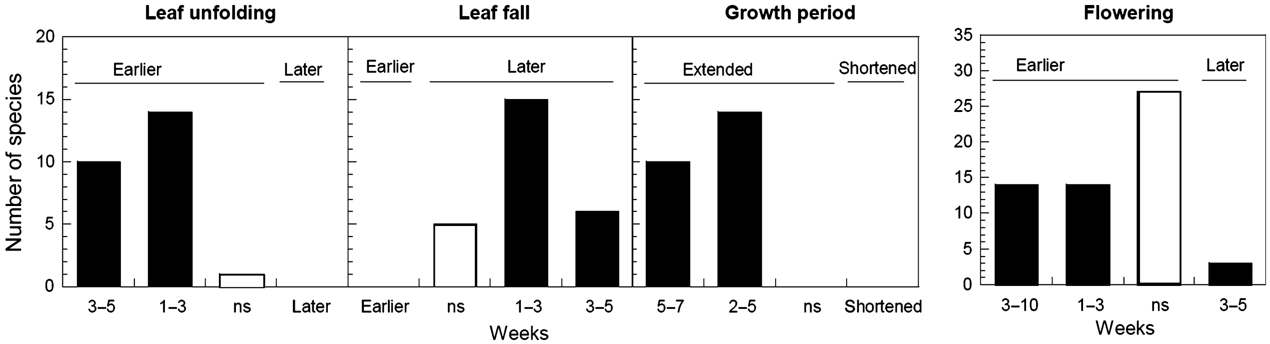

Fig. 3 Example of the phenological changes in the different species in the Montseny mountains (Catalonia, NE Spain) in the last 50 years of the 20th century. Based on Peñuelas *et al.* (2000a,b).

summer peak (Sherry *et al.*, 2007). Among the species that flower before the summer peak, the species that flower early tend to lengthen the duration of flowering by flowering earlier, whereas late-flowering species tend to advance the onset of flowering without increasing its duration (Giménez-Benavides *et al.*, 2011). These different shifts in plant phenology also produce a mismatch in species involved in the same biotic relationships, leading to disequilibrium in the sizes of populations (Both *et al.*, 2006). Mismatches have been singularly observed in mutualistic plant-pollinator relationships (Memmott *et al.*, 2007; Hoover *et al.*, 2012) and in plant–herbivore relationships (Post *et al.*, 2008; Green, 2010).

The specific phenological response of plants to drought has been less studied despite its important role (Peñuelas *et al.*, 2004b). Peñuelas *et al.* (2004b) found that the onset of greenup in the Iberian Peninsula shifts from spring (triggered by rising temperatures) in the northern cool-wet regions to autumn (triggered by the arrival of autumn rain) in the southern warm-dry regions. In water-limited ecosystems such as the Mediterranean ecosystems, experimental drier conditions (15–29% reduction in soil moisture) delayed the flowering period and decreased the number of flowers per plant (Ogaya & Peñuelas, 2004; Llorens & Peñuelas, 2005; Prieto *et al.*, 2008). This effect frequently had different intensities depending on the species in the studied community (Ogaya & Peñuelas, 2005). In contrast, in ecosystems of central Europe not limited by water, drought advanced the flowering period (Jentsch *et al.*, 2009). Because drought plays a key role in several parts of the world, intensive research on the phenological shifts it induces in plants and animals is warranted.

Warming also has significant direct effects on animal phenology by lengthening the period of summer activity and by increasing the number of reproductive cycles and larval size in insects (Stefanescu *et al.*, 2003; Harada *et al.*, 2005; Altermatt, 2010) or by changing the sex ratios in populations of turtles (Tucker *et al.*, 2008). In amphibians and birds, advanced periods of breeding and oviposition in response to warming have been observed (Beebee, 1995; Crick *et al.*, 1997; Schaefer *et al.*, 2006; Potti, 2009). An increase in reproductive success has been observed in reptiles (Zhang *et al.*, 2009; Takeda *et al.*, 2010; Clarke & Zani, 2012) and is frequently accompanied by an advance in the period of oviposition (Zhang *et al.*, 2009). Drought can have the opposite phenological effect to that of warming, for example, it has delayed phenological phases in butterflies of the Mediterranean basin (Stefanescu *et al.*, 2003).

The species-specific phenological responses of animals of the same community can be very different, with further consequences for biotic relationships (Stefanescu *et al.*, 2003). Guo *et al.* (2009), studying grasshoppers in Inner Mongolia, observed that the mid- and late-season species tended to advance the reproductive period, overlapping it with the early-season species, thus increasing the competition among different species of grasshoppers. In the Mediterranean Basin, with an expected increase in aridity, the varying degrees of phenological flexibility among species may account for differences in species' responses and, in the case of multivoltine species, strong selection is projected, favoring local seasonal adaptations such as diapauses or migratory behavior (Stefanescu *et al.*, 2003). In climates that are already warm, an enhanced warming can be important for ectothermic animals whose thermoregulative behavior can be critical for buffering the impact of severe warming (Kearney *et al.*, 2009).

The phenology of endothermic animals has also been affected by warming. The Alpine marmot has advanced its emergence from hibernation, leading to an earlier weaning of young and a longer growth season that thereafter imply larger body sizes before the next hibernation (Ozgul *et al.*, 2010). This larger body size favors a decline of adult mortality and a shift in the phenotypic composition of populations, which in turn triggers an abrupt increase in population size, thus showing that a phenological shift can cause sudden changes in evolution and demography (Ozgul *et al.*, 2010).

From individual changes to changes in populations, communities and ecosystems

The plasticity and degree of each individual to present intense responses at molecular, physiological, phenological and morphological levels are the first 'resources' to cope with the new climatic situation. Several studies, however, have observed that the responses of organisms are unable to prevent defoliation, decreases in growth, mortality, migration and shifts in the distributions of species (Peñuelas & Boada, 2003; Peñuelas *et al.*, 2007a,b, 2008b; Allen *et al.*, 2010; Carnicer *et al.*, 2011). Moreover, these responses at the level of individual organisms differ among individuals and species of the same community (Ogaya & Peñuelas, 2006; Volder *et al.*, 2010; Kardol et al., 2010; Ogaya *et al.*, 2011), implying further changes in community composition and feedback effects on climate change. We now discuss these impacts of climate change at the scales of populations, communities and ecosystems.

Responses of populations

Genotypic adaptation: microevolution

Plants can tolerate environmental changes '*in situ*' by a combination of phenotypic plasticity and genotypic adaptation (Jump & Peñuelas, 2005). The existence and magnitude of phenotypic plasticity, however, is under genetic control and is not unlimited (Jump & Peñuelas, 2005). Evidence suggests that phenotypic plasticity is submitted to strong selection pressure in the range limits of species distribution by the need of species communities to adapt to extreme conditions for the species (Fallour-Rubio *et al.*, 2009; Mátyás *et al.*, 2008). Phenotypic plasticity is thus likely to be under strong directional selection under climate change (Jump & Peñuelas, 2005).

Recent evidence links the genetic diversity of populations to population persistence in rapidly changing environments in wild ecosystems (Jump & Peñuelas, 2005; Eveno *et al.*, 2008; Jump *et al.*, 2008) (Fig. 4) and also relates genetic variability with climatic gradients (Elboutahiri *et al.*, 2010; Carnicer et al., 2012). Genomic approaches have become a potent tool for detecting alterations in population genetics (Luikart *et al.*, 2003; Storz, 2005; Bonin, 2008; Karrenberg & Widmer, 2008). With these techniques, the variation among individuals of the same population in the ability to establish under enhanced drought conditions has been observed in the Mediterranean shrub *Fumana thymifolia* (Jump *et al.*, 2008) and in *Pinus pinaster* (Eveno *et al.*, 2008). Direct rapid evolution toward drought avoidance was demonstrated in populations of *Brassica rapa*, where genotypes sampled after a multiyear drought showed significantly earlier flowering than did pre-drought individuals sampled from the same population (Franks *et al.*, 2007). Similarly, correlation between temperature and allele frequencies and directional changes in allele frequency in response to recent warming has been observed in populations of *Fagus sylvatica* (Jump *et al.*, 2006a). These and other similar examples suggest that, at least in some cases, climate-linked genotypic variation exists, and that plant species can respond to selection on a timescale relevant for responding to the current rapid anthropogenic environmental changes (Barrett & Schulter, 2008; Hoffmann & Willi, 2008; Jay *et al.*, 2012). This microevolutionary process has also been demonstrated in laboratory mesocosmic experiments studying the rapid microevolution of life-history traits (van Doorslaer *et al.*, 2007) and in field experiments where several loci presented significantly different frequencies in plants submitted to drought than in control plants (Jump *et al.*, 2008) (Fig. 4).

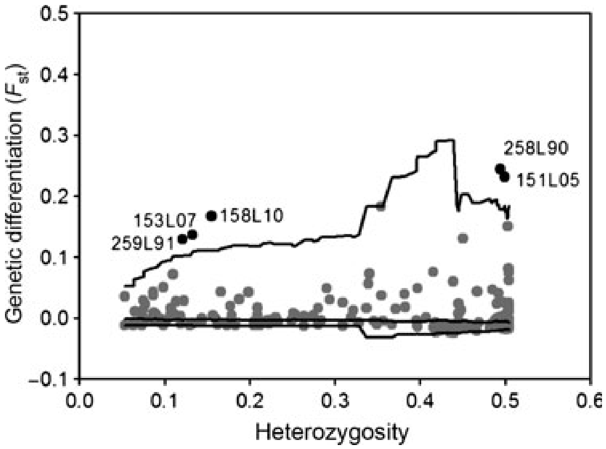

Fig. 4 Genetic differentiation between *Fumana thymifolia* individuals established in experimental drought and control treatments, based on AFLP molecular markers. The numbered loci are significantly more differentiated than would be expected if selectively neutral, indicating that selection resulting from elevated drought has resulted in changes in gene frequencies at these loci in the experimental treatment. Based on Jump *et al.* (2008).

Shifts in genetic composition in populations of birds are involved in recent changes in morphology and migration behavior related to climate changes (Pulido & Berthold, 2004). The presence of additive genetic variation within and among bird populations, and examples of rapid evolutionary responses to rare climatic events, suggest that birds also have a high potential for evolutionary change (Pulido & Berthold, 2004). Evolutionary adaptation can thus be rapid and can potentially help species to adapt to the current rapid changes in climate (Hoffmann & Sgrò, 2011), although the effectiveness of the evolutionary response to counter the negative impacts of rapid warming is generally expected to be rather more limited (Jump & Peñuelas, 2005).

Because different genotypes of the same species can differ in their functional traits in different environmental conditions, maintaining diversity within populations is likely to maximize the probability that the population will include the more adequate phenotypes in each different situation. Even though selection will lower the genotypic diversity of the population over time in a stable environment, gene flow and environment-dependent differences in fitness between genotypes interact with fluctuating selection pressures in a heterogeneous environment to maintain genotypic population diversity (Gutschick & BassiriRad, 2003). The loss of genetic variability elevates the vulnerability of populations to rapid environmental change (Esquinas-Alcázar, 2005; Hoffmann & Willi, 2008; Salvaudon *et al.*, 2008; Jump *et al.*, 2009a,b). Strong initial selection pressure in response to an environmental change, however, can also reduce genetic variability and the capacity of further adaptation if the environment continues to change (Newman & Pilson, 1997; Frankham, 2005; Leimu *et al.*, 2006; Endels *et al.*, 2007).

Despite the possible confusion between genotypic and plastic phenotypic responses in some studies, an increasing number of studies have observed signatures of rapid climate change on the microevolutionary response of populations (Gienapp *et al.*, 2008). The microevolution of a population in response to climate change is frequently related mainly to adaptation to altered seasonal events, such as drought or changes in seasonal length, rather than to the direct effect of a change in temperature (Bradshaw & Holzapfel, 2006). For example, in the study of *Brassica rapa* by Franks *et al.* (2007) referred to above, increases of multiyear droughts have induced microevolution in genotypes of *Brassica rapa* that has advanced the onset of flowering between 1.9 and 8.6 days relative to ancestral (predrought) phenotypes when both groups are grown under the same conditions.

Warming has impacts on insect populations living on the border of the species' distribution (Scriber, 2011). For example, in *hybrid zones* – the contact points between closely related and interfertile species, elevated genetic diversity and the disruption of gene complexes through recombination between different but genetically proximate species can open the way to rapid adaptation and speciation in response to environmental changes (Scriber & Ording, 2005; Scriber, 2011). The faster and more frequent shifts in species distributions under climate change can increase this type of speciation, potentially helping populations to adapt to changes in environmental gradients (Scriber, 2011).

Future studies should expand our knowledge of the interplay between plastic phenotypic, genotypic and epigenetic changes in the adaptation of organisms to current climate change (Hedhly *et al.*, 2008). Further research is required to identify both appropriate short- and long-term data sets for a range of species, traits and suitable analytical methods, which will permit the study of the complex interaction between phenotypic plasticity and genetic adaptation of organisms and their populations in response to climate change. Climate change constitutes an outstanding opportunity for genetic and evolutionary ecologists to advance our knowledge of the links, tuning and trade-offs among phenotypic plasticity, genotypic variability and population structure in the evolutionary success of species.

Changes in distribution and migration

There is accumulating evidence of changes in the distribution of organisms in response to climatic changes. In plants, the shifts currently most widely observed are those due mainly to drought interacting with hot summers that increase the limitation of water and erode the trailing range edge populations of a species, resulting in a contraction of its distribution toward wetter and cooler higher latitudes and altitudes (Pigott & Pigott, 1993; Allen & Breshears, 1998; Colwell *et al.*, 2008; Kullman, 2008; Jump *et al.*, 2009a,b; Harrison *et al.*, 2010) or due to elevated temperatures that allow population expansion at the leading range edge (Walther, 2003; Peñuelas *et al.*, 2007a,b; Kullman, 2008; Crimmins *et al.*, 2009; Jump *et al.*, 2009a,b). Range shifts, therefore, occur due to the combination of population expansion at the leading edges of distributions, through increased reproduction and establishment, and retraction at the trailing edges driven by elevated mortality and declines in growth and reproduction (Allen & Breshears, 1998; Peñuelas & Boada, 2003; Jump *et al.*, 2006a,b, 2007, 2009a; Peñuelas *et al.*, 2007a,b; Colwell *et al.*, 2008; Worrall *et al.*, 2008). More favorable climatic conditions can produce a shift in plant populations within the same altitudinal level across different montane aspects, from unfavorable to the most favorable climatic conditions resulting from differences in the hours of direct sunlight (Diemer, 2002). However, under more favorable climatic conditions for survival, range expansions are not inevitable as the shifting of the leading edge also depends on biotic factors such as herbivore pressure (Munier *et al.*, 2010) and dispersal dynamics (Fordham *et al.*, 2012).

Although distributional shifts are predicted along both latitudinal and altitudinal gradients, several physical and climatic factors have different patterns of variation in altitude than in latitude, such as partial CO_2 pressures and UV radiation. Furthermore, the physical distance necessary to reach sites with significantly different temperatures and/or pluviometry is measured in meters in altitude as opposed to similar changes occurring over kilometers along latitudinal transects (Körner, 2007). The isolation of populations of once widespread species and their retention in locally favorable sites can result in the formation and persistence of relict populations. In both lowland and mountainous areas, the presence of local variations in soil, microclimate and topographic heterogeneity, despite regionally unfavorable climates, can increase the resilience and resistance of local populations despite wider population declines (Ashcroft *et al.*, 2009; Godfree *et al.*, 2011; Hampe & Jump, 2011). Such increased isolation can also increase population divergence, resulting in the independent evolution of populations of a formerly more cohesive distribution (Jump & Peñuelas, 2005, 2006).

In animals, an increasing number of studies have shown changes in species distributions related to warming and drought (Guo *et al.*, 2009; Lenoir *et al.*, 2010; Kocsis & Hufnagel, 2011). Because of their higher mobility, animals have a greater capacity than plants to escape unfavorable climatic conditions. Despite the capacity of ectothermic animals such as insects to adapt, they present a 'heat-scape' temperature, described as the temperature that drives the insect to leave a site (Ma & Ma, 2012). This temperature differs among species of insects, suggesting that the composition of species communities under warming can change largely because of the different rates of migration of the different species (Ma & Ma, 2012). Changes in migration at regional scales have been observed in some groups of insects. For example, in butterflies, poleward shifts associated with regional warming have been observed in some species in Europe (Parmesan *et al.*, 1999).

In vertebrates, the rates of migration within a species sometimes differ with genotype, favoring the possibility of allopatric speciation such as observed in populations of the lizard *Lacerta vivipera* (Lepetz *et al.*, 2009). Birds can migrate in response to other human-driven effects, such as changes in land use, and/or by changes in biotic relationships related to warming (Lenoir *et al.*, 2010). However, the controversy over whether or not the changes in migratory behavior, for example in the long-distance migration of birds, are due to genotypic evolution remains (Both, 2007). Finally, the number of limitations and constraints of latitudinal shifts are large, from geographic natural barriers and lack of adequate food sources to human-driven constraints such as urbanization and habitat conversion (Jump *et al.*, 2009a, b). Consequently, and due to both natural and anthropogenic causes, each of these altitudinal and latitudinal shifts in plant species has its own peculiarities such that individual rates of migration will have impacts at the level of the community (Huntley, 1991).

Mortality and local extinction

Disturbance of species interactions, together with the low probability that phenotypic, genotypic and migrational responses will allow most species to tolerate rapid climate change, suggest a range-wide increase in individual mortality (Peñuelas *et al.*, 2000b) and therefore in the risk of local extinction (Jump & Peñuelas, 2005).

Furthermore, extreme temperatures in summer, which further exacerbate drought, increase dieback and reproductive failure in large areas on a continental scale (Peñuelas *et al.*, 2000b; Saxe *et al.*, 2001; Breshears *et al.*, 2005; Körner, 2007; Fensham *et al.*, 2009; Peng *et al.*, 2011). These dieback events by extreme climate changes are occurring with increasing frequency worldwide (Allen, 2009; Allen *et al.*, 2010). The threat of local extinction is even higher for species living in sites with restrictions to geographic shifts of populations toward more favorable areas, such as the higher altitudes of mountains (Rull & Vegas-Vilarrubia, 2006; La Sorte & Jetz, 2010), but this threat can be buffered by the presence of high topographic variability that allows suitable microclimates or sites with suitable soils (Peñuelas *et al.*, 2000b; Ashcroft *et al.*, 2009; Scherrer & Körner, 2011).

Defoliation and dieback thus increase when the phenotypic and genotypic capacity and the capacity of population movement are insufficient to cope with the climate change (Ogaya & Peñuelas, 2007a; Carnicer *et al.*, 2011) (Fig. 5). The consequenses of exceeding such tolerance thresholds are evident from historical data in the Mediterranean area showing substitution of forest by shrublands and deserts in relatively short periods of time (Estiarte *et al.*, 2008b) (Fig. 6).

Particular traits of species can render some species especially resistant or vulnerable to the risk of extinction. For example, *Phillyrea latifolia* can withstand warming and drought in Mediterranean forests much better than *Quercus ilex* because it dissipates excess radiation better and has stronger hydraulic resistance and higher WUE (Peñuelas *et al.*, 1998, 2000a,b). In another example, Iszkulo *et al.* (2009) have observed a

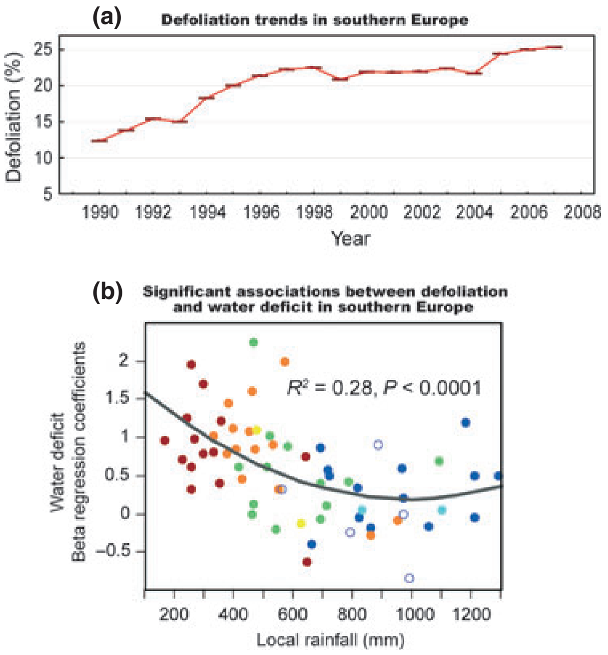

Fig. 5 (a) Increased defoliation in southern European forests in recent decades. (b) Defoliation in the Iberian Peninsula modeled as a function of water deficit (Emberger index) in generalized linear mixed models for each tree species in areas of different mean annual rainfall (i.e., rainfall quantiles). Significant coefficients of regression (β values) between water deficit and defoliation are plotted. The red dots represent beta values for 0–25 rainfall quantiles; orange dots, 25–50 quantiles; yellow dots, 0–50 quantiles; green dots, 50–75 quantiles; dark-blue dots, 75–100 quantiles; light-blue dots, 50–100 quantiles; white dots, species of restricted geographical distribution. Based on Carnicer *et al.* (2011).

large intolerance to drought in females of *Taxus baccata*, which strongly reduces the reproductive success of the species and makes it especially vulnerable to extinction in areas under increased drought.

Highly diverse ecosystems are sensitive to losses of biodiversity in response to warming and drought (van Peer *et al.*, 2004). Because of their high biodiversity, tropical forests particularly suffer from the impacts of the current rapid climate change. Moreover, a reduction in the availability of water has a large impact on tropical forests because of the long-term adaptations of their organisms to high temperatures and availability of water. Current models project a high risk of losses of biodiversity in tropical forests by warming (Malcolm *et al.*, 2005). In the dry tropical forests of Central America, a rapid increase in drought by the lengthening of the drought season by 4 weeks can cause the extinction of 25–40% of forest species (Condit, 1998). Sensitivity may also be high in temperate or boreal systems of low diversity, however, when dieback occurring in the two main species forming the canopy may generate strong transformations at the ecosystemic scale, from forest to shrubland, for example.

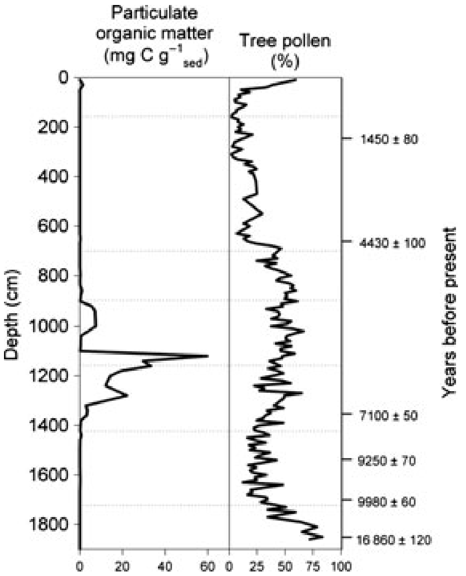

Fig. 6 Changes in the land cover from forest to shrubland in southern Spain in the last millennium. Based on Estiarte *et al.* (2008b).

Elevated temperatures can directly threaten the survival of populations by restricting migration to higher altitudes (Shoo *et al.*, 2005). Populations of tropical animals, particularly of ectotherms such as insects and reptiles, are especially threatened under warming because they currently live very close to their optimal temperatures. Those species that live in sites with limited possibilities for migration, such as mountainous areas or islands, have a high risk of local extinction (Chiu *et al.*, 2012).

Changes in communities

Through changes in abiotic factors

Apart from drought and warming themselves, one frequently observed abiotic effect of climate change is the shift in availability of soil nutrients (Hobbie & Chapin, 1996; Shaver *et al.*, 2000; Schmidt *et al.*, 2002; Beier *et al.*, 2008; Li *et al.*, 2011d; Sardans *et al.*, 2012b). Because organisms frequently respond to climate change by shifting their chemical composition and use of resources (Sardans *et al.*, 2012b), they can exert an effect on ecosystemic C, N and P cycles that thereafter can produce feedback effects on the community species that must respond to these cycles (Finzi *et al.*, 2011). Drought decreases the activities of soil enzymes (Garcia *et al.*, 1994; Sardans & Peñuelas, 2005, 2010; Sardans *et al.*, 2008b,c) and the turnover and availability of nutrients (Sardans & Peñuelas, 2004, 2007; Bloor & Bardgett, 2012), effects that generate changes in the elemental composition of plants that vary in intensity in the different species of the plant community (Sardans *et al.*, 2007; Peñuelas *et al.*, 2008a). For example, a relative increase in fungal vs. bacterial dominance in soil communities has been repeatedly reported in response to drought (Yavitt *et al.*, 2004; Yuste *et al.*, 2011).

In cold and wet temperate areas, warming frequently increases the decomposition of soil organic matter (Schmidt *et al.*, 2002; Wessel *et al.*, 2004; Gornall *et al.*, 2009; Butler *et al.*, 2012), availability of soil nutrients (Beier *et al.*, 2008; Aerts, 2010), plant growth (Molau, 1997; Hill & Henry, 2011) and biomass of the soil community and leads to changes in its species composition (Sjursen *et al.*, 2005; Zhang *et al.*, 2005b; Schulte *et al.*, 2008; Yergeau *et al.*, 2012) . These changes provide new competitive scenarios both among plants (Gornall *et al.*, 2009) and between plants and microbes (Schmidt *et al.*, 2002).

Warming can also change the relationships of interspecific competition by changing the structure of the physical habitat. For example, sympatric species of penguins have changed their competitive equilibrium as a result of a reduction in the extent of sea ice produced by warming, which has a greater detrimental effect on species that depend on ice area for their reproduction and fishing (Forcada *et al.*, 2006).

Through biotic effects on the structure and function of trophic webs

The direct effects of climate change on the different species of a community also change the biotic relationships among the species. Species must therefore adapt to new scenarios of competitive and trophic relationships.

Warming can exert a direct effect on the relationships of interspecific competition because plant species of the same community frequently respond with different intensities in both their growth and their reproduction (Shaver *et al.*, 2000; Weltzin *et al.*, 2000, 2003; Walker *et al.*, 2006; Williams *et al.*, 2007; Prieto *et al.*, 2009b; Green, 2010; Verlinden & Nijs, 2010; Bokhorst *et al.*, 2008, 2011; Messaoud & Chen, 2011; Zhang *et al.*, 2011b; Reed *et al.*, 2012). In some cases, the increases in growth of some species are accompanied by decreases in growth in other species (Day *et al.*, 1999; Price & Waser, 2000; Cornelissen *et al.*, 2001; Walker *et al.*, 2006; Gebler *et al.*, 2007). These asymmetrical effects are further related to competitive suppression (Kudo & Suzuki, 2003; Reed *et al.*, 2012) and decreases in the diversity of species in plant communities (Farnsworth *et al.*, 1995; Cornelissen *et al.*, 2001; Klein *et al.*, 2004; Walker *et al.*, 2006; Cross & Harte, 2007; Gedan & Bertness, 2009; Prieto *et al.*, 2009d; Lang *et al.*, 2012a). Some groups, for example lichens, are more prone to extinction in cold areas submitted to warming (Wahren *et al.*, 2005; Walker *et al.*, 2006). The loss of biomass from the disappearance of some species is frequently compensated by an increase in growth of the remaining species (Cross & Harte, 2007). For example, the loss of biomass and diversity in lichens of arctic ecosystems is related to increases in the biomass and diversity of shrubs and herbs (Wahren *et al.*, 2005; Walker *et al.*, 2006; Joly *et al.*, 2009). Warming increases interspecific competition and discourages the establishment of new plant species, especially when the community is highly diverse (Klanderud & Totland, 2007) potentially limiting population expansion for some species.

Warming has bottom-up effects. The plant–herbivore relationship is one of the most important biotic relationships. It depends on the coordination between plant and herbivore phenology (Loe *et al.*, 2005). Outbreaks of insects are likely to increase under global warming due to the direct effects of higher temperatures on these ectothermic animals (Tobin *et al.*, 2008; Jönsson *et al.*, 2009) and to the extension of their active periods (Tobin *et al.*, 2008; Jönsson *et al.*, 2009). The changes in phenology and distribution caused by warming can also asymmetrically affect herbivores and predators (Barton, 2010); predators can compensate for the decrease in encountering herbivores by increasing their activity (Lang *et al.*, 2012b). Some long-term field and laboratory studies suggest that warming disproportionally affects the loss of top predators and herbivores compared to autotrophs and microbes (Petchey *et al.*, 1999).

A paradigmatic case of indirect biotic alteration resulting from the effects of warming on plant and animal metabolism is that produced by the increase in biogenic volatile organic emissions (BVOCs). This increase varies depending on the plant (and animal) species and the phenological and ontogenic stage, but it is also different for the hundreds or thousands of different BVOCs emitted by plants. As a result, significant changes occur in the protection of plants from climatic stresses, the communication between plants and pollinators, the relationships among plants and with herbivores and the defense of plants from pathogens, among others (Peñuelas & Staudt, 2010; Llusia *et al.*, 2010, 2011) (Fig. 7). Significant changes in the competitive abilities of species are highly likely to result in changes in the composition of communities (Peñuelas & Staudt, 2010).

Warming can also exert indirect effects on communities by top-down mechanisms. Warming can increase the activities of predators and change hunting strategies between pursuit and wait/ambush, which changes the competitive pressures on different species of predator and drives some to extinction (Barton & Schmitz,

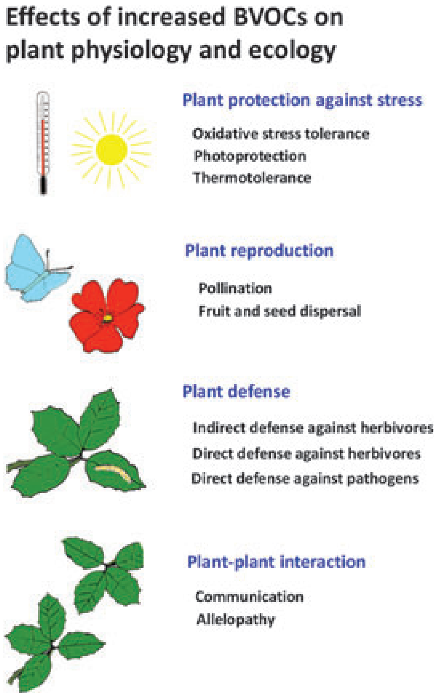

Fig. 7 Flow-on effects of warming on community processes through changes in plant BVOC emissions. Based on Peñuelas & Staudt (2010).

2009). Increases in herbivore pressure can have complex effects on community structure as increases in herbivore activity under warming are frequently asymmetrical, with most herbivores increasing their activity while others decrease theirs (Rizhsky *et al.*, 2004). Populations of bark beetles in the boreal forests of Canada have grown because the number of stressed and ill trees, which are sources of food for these herbivores, have increased under warming, a situation that impacts the entire boreal community (Choi, 2011). A higher activity of herbivores can asymmetrically impact different plant species and thus change the scenarios of competition among them (Van Bogaert *et al.*, 2009). The gregarious behavior of North American wolves in some areas varies depending on the intensity of winter snow. In years with more snow, wolves hunt more efficiently in large groups and can triple the number of deer killed compared to years with less snow when the wolves hunt in smaller groups. Deer populations thus rise in years with less snow, and the understory of the fir forest decreases, whereas contrary top-down effects occur in years with high snow cover (Post *et al.*, 1999). The decreases in understory vegetation generated by a high presence of deer in years of low snowfall also decrease the populations of songbirds (Martin & Maron, 2012).

Drought can also change the competitive relationships in arid areas because the capacities and strategies of plant species to adapt to drought are different, as reported in several observational and experimental studies (Llorens *et al.*, 2003; Ogaya & Peñuelas, 2003, 2005, 2006, 2007a; Lloret *et al.*, 2004a,b; Loe *et al.*, 2005; Ripley *et al.*, 2010; Belerkuhnlein *et al.*, 2011). In this new scenario of plant interspecific competition, species less able to adapt to drought can be eliminated. Long-term experimental studies are needed to determine whether species whose production, flowering or growth are negatively impacted by drought have compensatory mechanisms, for example by enhancing their defensive capacity against herbivores or their competitive ability against neighboring plants through chemical allelopathy. Compensatory mechanisms can help these initially disfavored species to remain, perhaps with lower density, in their current ranges under drought conditions. Plant defenses such as phenolics increase under warming (Scriber, 2011) and drought (Hale *et al.*, 2005; Atala & Gianoli, 2009) and can then act as deterrents to herbivores (Eichhorn *et al.*, 2007; Cipollini *et al.*, 2008). Drought frequently has bottom-up effects that impact on plant cover and reduce species richness (Tilman & Haddi, 1992; Lloret *et al.*, 2004b, 2009; Yurkonis & Meiners, 2006; Reed *et al.*, 2012). Drought reduces the quality and abundance of host plants, thereby reducing herbivore populations (Sumerford *et al.*, 2000) and affecting the entire trophic web (Sumerford *et al.*, 2000; Pritchard *et al.*, 2007). Drought can also have strong top-down effects. In Mediterranean regions, drought has been related to the loss of insect species, especially of specialist insects (Stefanescu *et al.*, 2011). The trade-offs between defenses to drought and to herbivores remain unclear but seem quite variable (Haugen *et al.*, 2008; Gutbrodt *et al.*, 2012).

Ecosystems

Climatic feedbacks

When changes in phenology and plant communities are large, at regional and continental scales, they can exert significant feedback effects on climate (Peñuelas *et al.*, 2009b) (Fig. 8). Lengthening the period of plant activity can increase the uptake of atmospheric CO_2 (Peñuelas & Filella, 2001), thereby buffering the increased levels of CO_2. Despite the lengthening of plant activity, the increase in frequency and severity of drought seems to have precluded the expected increase in tree growth worldwide (Peñuelas *et al.*, 2011a,b) and in the fixation of CO_2 (Angert *et al.*, 2005; Ciais *et al.*, 2005; Buermann *et al.*, 2007; Zhao & Running, 2010). The emissions of plant BVOCs also increase with temperature and longer periods of plant activity (Peñuelas & Llusia, 2003; Peñuelas *et al.*, 2005; Blanch *et al.*, 2007, 2011) (Fig. 8). Although their atmospheric lifetime is short, BVOCs have an important influence on climate through the formation of aerosols that can cool the Earth's surface during the day by intercepting solar radiation (Claeys *et al.*, 2004; Kullman, 2008) (Fig. 9). Moreover, a longer presence of green cover should influence other factors such as albedo, latent and sensible heat and atmospheric turbulence (Peñuelas *et al.*, 2009b). In some areas of North America, spring temperatures are different after leaf emergence due to increases in latent heat (Schwartz, 1996; Fitzjarrald *et al.*, 2001). Moreover, the denser the cover, the higher the turbulence and latent heat, leading to a cooler and wetter atmospheric boundary layer (Bonan, 2008). Increasing the duration of green cover can thus generate a cooling by sequestering more CO_2 and by increasing evapotranspiration. On the other hand, higher plant production and increased evapotranspiration decrease soil moisture and may generate abrupt rises of temperature when drought precludes evapotranspiration. An early and prolonged green period with increased evapotranspiration may have enhanced recent summer heat waves in Europe by lowering soil moisture (Zaitchik *et al.*, 2006; Fisher *et al.*, 2007). Decreases of soil moisture have a negative effect on late cooling and consequently increase surface temperature (Fisher *et al.*, 2007) and probably reduce summer precipitation (Jentsch *et al.*, 2009).

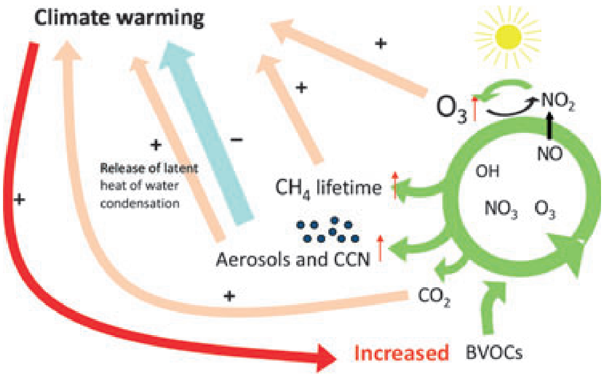

Fig. 8 Flow-on and feedback effects of warming on atmospheric processes through changes in plant BVOC emissions. Based on Peñuelas & Staudt (2010).

All these feedbacks generated by the lengthening of the period of plant growth are also generated by permanent changes in communities and ecosystems that also change the vegetative cover. For example, the shifts from forest to shrubland or to grassland described above as responses to climate change (e.g., Estiarte *et al.*, 2008b) must have significant biophysical (albedo, latent heat, sensible heat) and biogeochemical (e.g., decreased CO_2 fixation, changed BVOC emission, altered exchanges of greenhouse gases) feedbacks (Bonan, 2008).

One of these feedbacks, which may be the key feedback affecting climate change, is the changing role of ecosystems in the fixation of CO_2. We have yet to discern whether the current widespread summer droughts negate the enhancement of CO_2 uptake induced by

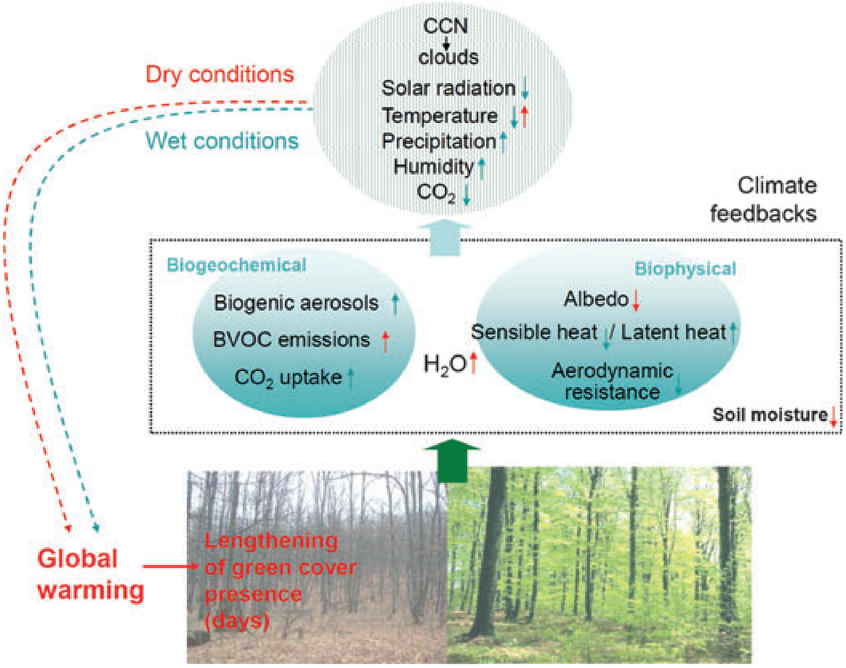

Fig. 9 Feedbacks on climate of the lengthening of the growth period in response to global warming. Based on Peñuelas *et al.* (2009a).

warmer springs, possibly by CO_2 fertilization or increased eutrophication. An accurate continuous quantification of the role of ecosystems as carbon sinks and the changes produced by climate change constitutes a key issue in the face of ongoing disturbance. Current tools for the continuous monitoring of carbon uptake by ecosystems include eddy covariance and remote sensing. Eddy covariance is currently the only direct way to assess the carbon flux of whole ecosystems with high temporal resolution. Nevertheless, towers for eddy covariance can effectively measure a single 'point' over flat and uniform terrain, usually on a scale of a few square kilometers or less (Baldocchi, 2003). Remote sensing has, instead, the ability to extend the spatial coverage of observations of carbon flux beyond a fixed point. Promising approaches include the use of the Photochemical Reflectance Index (PRI) (Garbulsky *et al*., 2011; Peñuelas *et al*., 2011a,b) or of fluorescence (Frankenberg *et al*., 2011) that offer good prospects for the continuous global monitoring of plant primary productivity from space (Fig. 10).

Conclusions and perspectives for future research

These many lines of evidence indicate that current climate change is having a great impact on organisms, populations, communities and terrestrial ecosystems by changing phenotypes, genotypes, growth, phenology, the distribution of organisms, species competitive ability, ecological relationships and the risk of extinction in communities. Ecosystems are thus changing in structure and function and have significant feedbacks on climate change itself.

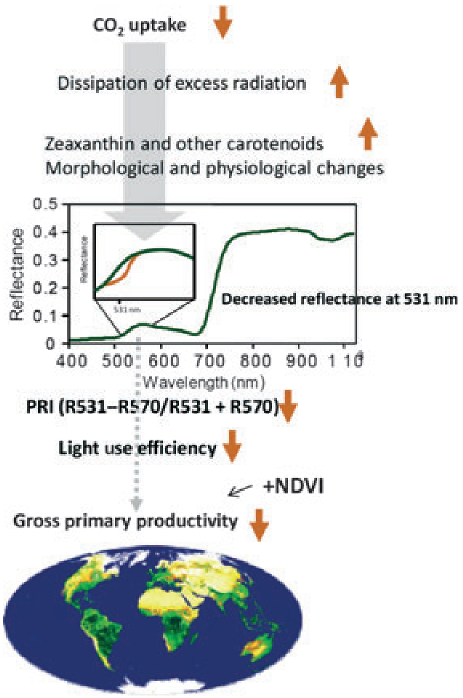

Fig. 10 Photochemical Reflectance Index (PRI) as a possible monitor of gross primary productivity everywhere all the time. Based on Peñuelas *et al.* (2011b). NDVI Normalized difference vegetation index or similar index providing a proxy of absorbed radiation by green biomass.

We know less about how these primary responses affect the capacity of organisms, populations, communities and ecosystems to respond to the interactions with the other simultaneous stresses produced by other drivers of global change and to the new biotic relationships that are generated. As one example among many of the interactions from global change, the current changes in the N : P ratios of organisms and environments, which some ecosystems are experiencing as a result of the unbalanced input to the biosphere by humans (Peñuelas *et al*., 2012), can strongly interact with climate change. We can hypothesize that in a scenario of drought, an increase in the N : P ratio can interact with the decrease in the availability of water, favoring species with low rates of growth and more conservative uses of resources. The N : P ratios can significantly affect the rate and direction of the responses of organisms, populations and communities to climate change, but no information about this possibility is available.

Current studies of field climatic manipulations interacting with eutrophication or elevated levels of CO_2, though, can help. They should continue as long as possible as many lines of evidence indicate that the longer in time and the wider in space the experiments are conducted, the more buffered are the changes described (Leuzinger *et al*., 2011). They must also be complemented with observational studies based on inventories (Carnicer *et al*., 2011), remote sensing data (Zhao & Running, 2010), paleoecological data (Estiarte *et al*., 2008b) and large data sets (Kattge *et al*., 2011) to shed light on the actual impacts climate change is having on life on Earth. The coupling of omic studies with studies of nutrient cycles, nutrient availability and stoichiometry, physiological and phenological changes and ecosystem structure shifts will allow making a step forward on our integrated understanding of the mechnisms and processes underlying biological impacts of climate change.

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References

Aerts R (2010) Nitrogen-dependent recovery of subartic tundra vegetation after simulation of extreme winter warming damage to *Empetrum hermaphroditum*. *Global Change Biology*, **16**, 1071–1081.

Aiba SI, Kitayama K (2002) Effects of the 1997–98 El Niño drought on rain forest of Mount Kinabalu, Borneo. *Journal of Tropical Ecology*, **18**, 215–230.

Alam I, Sharmin SA, Kim KH, Yang JK, Choi MS, Lee BH (2010) Proteome analysis of soybean roots subjected to short-term drought stress. *Plant and Soil*, **333**, 491–505.

Albert KR, Ro-Poulsen H, Mikkelsen TN, Michelsen A, Van der Linden L, Beier C (2011a) Effects of elevated CO2, warming and drought episodes on plant carbon uptake in a temperate heath ecosystem are controlled by soil water status. *Plant, Cell and Environment*, **34**, 1207–1222.

Albert KR, Ro-Poulsen H, Mikkelsen TN, Michelsen A, Van der Linden L, Beier C (2011b) Interactive effects of elevated CO_2, warming, and drought on photosynthesis of *Deschampsia flexuosa* in a temperate heath ecosystem. *Journal of Experimental Botany*, **62**, 4253–4266.

Alla MMN, Khedr AHA, Serag MM, Abu-Alnaga AZ, Nada RM (2012) Regulation of metabolomics in *Atriplex halimus* growth under salt and drought stress. *Plant Growth Regulation*, **67**, 281–304.

Allen CD (2009) Climate-induced forest diebach: an escalating global phenomenon? *Unasylva*, **231/232**, 43–49.

Allen CD, Breshears DD (1998) Drought-induced shift of a forest-woodland ecotone: rapid landscape response to climate variation. *Proceedings of the National Academy of Sciences of the United States of America*, **95**, 14839–14842.

Allen CD, Macalady AK, Chenchouni H *et al.* (2010) A global overview of drought and heat-induced tree mortality reveals emerging climate change risks for forests. *Forest Ecology and Management*, **259**, 660–684.

Altermatt F (2010) Climate warming increases voltilism in European butterflies and moths. *Proceedings of the Royal Society B*, **277**, 1281–1287.

Alvarez S, Marsh EL, Schroeder SG, Schachtman DP (2008) Metabolomic and proteomic changes in the xylem sap of maize under drought. *Plant, Cell and Environmental*, **31**, 325–340.

Angert A, Biraud S, Bonfils C *et al.* (2005) Drier summers cancel out the CO_2 uptake enhancement induced by warmer springs. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 10823–10827.

Aranjuelo I, Molero G, Erice G, Avice JC, Nogués S (2011) Plant physiology and proteomics reveals the leaf response to drought in alfalfa (*Medicago sativa* L.). *Journal of Experimental Botany*, **62**, 111–123.

Arft AM, Walker MD, Gurevitch J *et al.* (1999) Responses of tundra plants to experimental warming: meta-analysis of the international tundra experiment. *Ecological Monographs*, **69**, 491–511.

Arndt SK, Livesley SJ, Merchant A, Bleby TM, Grierson PF (2008) Quercitol and osmotic adaptation of field-grown *Eucalyptus* under seasonal drought stress. *Plant, Cell and Environmental*, **31**, 915–924.

Ashcroft MB, Chishol LA, French KO (2009) Climate change at the landscape scale: predicting fine-grained spatial heterogeneity in warming and potential refugia for vegetation. *Global Change Biology*, **15**, 656–667.

Asner GP, Nepstad D, Cardinot G, Ray D (2004) Drought stress and carbon uptake in a Amazon forest measured with space borne imaging spectroscopy. *Proceedings of the National Academy of Sciences of the United States of America*, **101**, 6039–6044.

Atala C, Gianoli E (2009) Drought limits induced twining by leaf damage in the climbing plant *Ipomoea purpurea* (L.) roth (Convolvulaceae). *Gayana Botanica*, **66**, 171–176.

Aubert Y, Vile D, Pervent M *et al.* (2010) RD20, a stress-inducible caleosin, participates in stomatal control, transpiration and drought tolerance in Arabidopsis thaliana. *Plant and Cell Physiology*, **51**, 1975–1987.

Badeck FW, Bondeau A, Böttcher K, Doktor D, Lucht W, Schaber J, Sich S (2004) Responses of spring phenology to climate change. *New Phytologist*, **162**, 295–309.

Baldocchi DD (2003) Assessing the eddy covariance technique for evaluating carbon dioxide exchange rates of ecosystems: past, present and future. *Global Change Biology*, **9**, 479–492.

Barret RDH, Schluter D (2008) Adaptation from standing genetic variation. *Trends in Ecology and Evolution*, **23**, 38–44.

Barton BT (2010) Climate warming and predation risk during herbivory ontogeny. *Ecology*, **91**, 2811–2818.

Barton BT, Schmitz OJ (2009) Experimental warming transforms multiple predator effects in a grassland food web. *Ecology Letters*, **12**, 1317–1325.

Barua D, Heckathorn SA, Coleman JS (2008) Variation in heat-shock proteins and photosynthetic thermobalance among natural populations of *Chenopodium album* L. from contrasting thermal environments: implications for plant responses to global warming. *Journal of Integrative Plant Biology*, **50**, 1440–1451.

Beebee TJC (1995) Amphibian breeding and climate. *Nature*, **374**, 219–220.

Beerling DJ (2002) Low atmospheric CO_2 levels during the Permo-Carboniferous glaciation in ferred from fossil lycopsids. *Proceedings of the National Academy of Sciences of the United States of America*, **99**, 12567–12571.

Beier C, Emmett BA, Peñuelas J *et al.* (2008) Carbon and nitrogen cycles respond differently to global warming. *Science of the Total Environment*, **407**, 692–697.

Belerkuhnlein C, Thiel D, Jentsch A, Willner E, Kreyling J (2011) Ecotypes of European grass species respond differently to warming and extreme drought. *Journal of Ecology*, **99**, 703–713.

Bernardo J, Ossola RJ, Spotila J, Crandall KA (2007) Interspecies physiological variation as a tool for cross-species assessments of global warming-induced endangerment: validation of an intrinsic determinant of macroecological and phylogeographic structure. *Biology Letters*, **3**, 695–698.

Berta M, Giovannelli A, Sebastiani F, Camussi A, Racchi ML (2010) Transcriptome changes in the cambial region of poplar (*Populus alba* L.) in response to water deficit. *Plant Biology*, **12**, 341–354.

Biasi C, Meyer H, Rusalimova O *et al.* (2008) Initial effects of experimental warming on carbón exchange rates. Plant growth and microbial dynamics of a lichen-rich dwarf shrub tundra in Siberia. *Plant and Soil*, **307**, 191–205.

Bigras FJ (2005) Photosynthetic response of white spruce families to drought stress. *New Forests*, **29**, 135–148.

Blanch JS, Peñuelas J, Llusià J (2007) Sensitivity of terpene emissions to drought and fertilization in terpene-storing *Pinus halepensis* and non-storing *Quercus ilex*. *Physiologia Plantarum*, **131**, 211–225.

Blanch JS, Llusia J, Niinemets Ü, Noe SM, Peñuelas J (2011) Instantaneous and historical temperature effects on α-pinene emissions in *Pinus halepensis* and *Quercus ilex*. *Journal of Environmental Biology*, **32**, 1–6.

Bloor JMG, Bardgett RD (2012) Stability of above-ground and below-ground processes to extreme drought in model grassland ecosystems: interactions with plant species diversity and soil nitrogen availability. *Perspectives in Plant Ecology, Evolution & Systematics*, **14**, 193–204.

Bloor JMG, Pichon P, Falcimagne R, Leadley P, Soussana JF (2010) Effects of warming, summer drought, and CO_2 enrichment on aboveground biomass production, flowering phenology, and community structure in an upland community structure in an upland grassland ecosystem. *Ecosystems*, **13**, 888–900.

Bokhorst S, Bjerke JW, Sowles FW, Melillo J, Callaghan TV, Phoenix GK (2008) Impacts of extreme winter warming in the sub-Artic growing season responses of dwarf shrub heathland. *Global Change Biology*, **14**, 2603–2612.

Bokhorst S, Bjerke JW, Street LE, Callaghan TV, Phoenix GK (2011) Impacts of multiple extreme warming events on sub-artic heathland: phenology, reproduction, growth and CO_2 flux responses. *Global Change Biology*, **17**, 2817–2830.

Bonan GB (2008) *Ecological Climatology: Concepts and Applications*, 2nd edn. Cambridge University Press, Cambridge.

Bonebrake TC, Deutsch CA (2012) Climate heterogeneity modulates impact of warming on tropical insects. *Ecology*, **93**, 449–455.

Bonhomme L, Monclus R, Vincent D *et al.* (2009) Genetic variation and drought response in two *Populus* × *euramericana* genotypes through 2-DE proteomic analysis of leaves from field and glasshouse cultivated plants. *Phytochemistry*, **70**, 988–1002.

Bonin A (2008) Population genomics: a new generation of genome scans to bridge the gap with functional genomics. *Molecular Ecology*, **17**, 3583–3584.

Borghetti M, Cinnirella S, Magnani F, Saracino A (1998) Impact of long-term drought on xylem embolism and growth in *Pinus halepensis* Mill. *Trees*, **12**, 187–195.

Both C (2007) Comment on "Rapid advance of spring arrival dates in long-distance migratory birds". *Science*, **315**, 598b.

Both C, Bouwhuis S, Lessells CM, Visser ME (2006) Climate change and population declines in a long-distance migratory bird. *Nature*, **441**, 81–83.

Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science*, **312**, 1477–1478.

Breshears DD, Cobb NS, Rich PM *et al.* (2005) Regional vegetation die-off in response to global-change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **102**, 15144–15148.

Brodribb T, Hill RS (1998) The photosynthetic drought physiology of a diverse group of southern hemisphere conifer species is correlated with minimum seasonal rainfall. *Functional Ecology*, **12**, 465–471.

Bronson DR, Gower ST, Tanner M, van Herk I (2009) Effect of ecosystem warming on boreal black spruce bud burst and shoot growth. *Global Change Biology*, **15**, 1534–1543.

Buermann W, Linter BR, Benjamin R *et al.* (2007) The changing carbon cycle at Mauna Loa observatory. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 4249–4254.

Butler SM, Melillo JM, Johnson JE *et al.* (2012) Soil warming alters nitrogen cycling in a New England forest: implications for ecosystem function and structure. *Oecologia*, **168**, 819–828.

Callaway RM, DeLucia EH, Schlesinger WH (1994) Biomass allocation of montane and desert ponderosa pine: an analog for response to climate change. *Ecology*, **75**, 1474–1481.

Carmo-Silva AE, Keys AJ, Beale MH *et al.* (2009) Drought stress increases the production of 5-hydroxynorvaline in two C4 grasses. *Phytochemistry*, **70**, 664–671.

Carnicer J, Coll M, Ninyerola M, Pons X, Sánchez G, Peñuelas J (2011) Widespread crown condition decline, food web disruption, and amplified tree mortality with increased climate change-type drought. *Proceedings of the National Academy of Sciences of the United States of America*, **108**, 1474–1478.

Carnicer J, Peñuelas J (2012) The world at a crossroads: Financial scenarios for sustainability. *Energy Policy*, **48**, 611–617.

Carnicer J, Brotons L, Stefanescu C , Peñuelas J (2012) Biogeography of species richness gradients: linking adaptive traits, demography and diversification. *Biological Reviews*, **87**, 457–479.

Carter EB, Theodorou MK, Morris P (1997) Responses of *Lotus corniculatus* to environmental change. *New Phytologist*, **136**, 245–253.

Caruso G, Cavaliere C, Foglia P, Gubbiotti R, Samperi R, Laganà A (2009) Analysis of drought responsive proteins in wheat (*Triticum durum*) by 2D-PAGE and MALDI-TOF mass spectrometry. *Plant Science*, **177**, 570–576.

Casper BB, Forseth IN, Wait DA (2006) A stage-based study of drought response in *Cryptantha flava* (Boraginaceae): gas exchange, water use efficiency, and whole plant performance. *American Journal of Botany*, **93**, 977–987.

Cernusak LA, Winter K, Turner BL (2011) Transpiration modulates phosphorus acquisition in tropical tree seedlings. *Tree Physiology*, **31**, 878–885.

Chang S, Puryear JD, Dilip MA, Dias L, Funkhouser EA, Newton RJ, Cairney J (1996) Gene expression under water deficit in loblolly pine (*Pinus taeda*): isolation and characterization of cDNA clones. *Physiologia Plantarum*, **97**, 139–148.

Chapin FS II, Shaver GR, Giblin AE, Nadelhoffer KJ, Laundre JA (1995) Responses of Arctic tundra to experimental and observed changes in climate. *Ecology*, **76**, 694–711.

Charlton AJ, Donarski JA, Harrison M *et al.* (2008) Responses of the pea (*Pisum sativum* L.) leaf metabolome to drought stress assessed by nuclear magnetic resonance spectroscopy. *Metabolomics*, **4**, 312–327.

Chiu MC, Chen YH, Kuo MH (2012) The effect of experimental warming on a low-latitude aphid, Myzus varians. *Entomologia Experimentalis et Applicata*, **142**, 216–222.

Cho SK, Ryu MY, Song C, Kwak JM, Kim WT (2008) Arabidopsis PUB22 and PUB23 are homologous U-Box E3 ubiquitin ligases that play combinatory roles in response to drought stress. *The Plant Cell*, **20**, 1899–1914.

Choi WI (2011) Influence of global warming on forest coleopteran communities with special reference to ambrosia and bark beetles. *Journal of Asia-Pacific Entomology*, **14**, 227–231.

Chuine I, Morin X, Bugmann H (2010) Warming, photoperiods and tree phenology. *Science*, **329**, 275–276.

Chuine I, Morin X, Sonié L *et al.* (2012) Climate change might increase the invasion potential of the alien C4 grass *Setaria parviflora* (Poaceae) in the Mediterranean Basin. *Diversity and Distributions*, **18**, 661–672.

Ciais P, Reichstein M, Viovy N *et al.* (2005) Europe-wide reduction in primary productivity caused by heat and drought in 2003. *Nature*, **437**, 529–533.

Cipollini D, Stevenson R, Enright S, Eyles A, Bonello P (2008) Phenolic metabolites in leaves of the invasive shrub, *Lonicera maackii*, and their potential phytotoxic and anti-herbivore effects. *Journal of Chemical Ecology*, **34**, 144–152.

Claeys M, Graham B, Vas G *et al.* (2004) Formation of secondary organic aerosols through photooxidation of isoprene. *Science*, **303**, 1173–1176.

Clarke DN, Zani PA (2012) Effects on nighttime warming on temperature ectotherm reproduction: potential fitness benefits of climate change for side-blotched lizards. *Journal of Experimental Botany*, **215**, 1117–1127.

Clarke LJ, Robinson SA, Hua Q, Ayre DJ, Fink D (2012) Radiocarbon bomb spike reveals biological effects of Antarctic climate change. *Global Change Biology*, **18**, 301–310.

Cohen D, Bogeat-Triboulot MB, Tisserant E *et al.* (2010) Comparative transcriptomic of drought responses in Populus: a meta-analysis of genome-wide expression profiling in mature leaves and root apices across two genotypes. *BMC Genomics*, **11**, 630.

Colwell RK, Brehn G, Cardelús CL, Gilman AC, Longino JT (2008) Global warming, elevational range shifts, and lowland biotic attrition in the wet tropics. *Science*, **322**, 258–261.

Condit R (1998) Ecological implications of changes in drought patterns: shifts in forest composition in Panama. *Climate Change*, **39**, 413–427.

Corcuera L, Camarero JJ, Gil-Pelegrín E (2004) Effects of severe drought on *Quercus ilex* radial growth and xylem anatomy. *Trees*, **18**, 83–92.

Cornelissen JHC, Callaghan TV, Alatalo JM *et al.* (2001) Global change and arctic ecosystems: is lichen decline a function of increases in vascular plant biomass? *Journal of Ecology*, **89**, 984–994.

Cramer MD, Hawkins Verboom GA (2009) The importance of nutritional regulation of plant water flux. *Oecologia*, **161**, 15–24.

Cramer GR, Ergül A, Grimplet J *et al.* (2007) Water and salinity stress in grapevines: early and late changes in transcript and metabolite profiles. *Functional Integrative Genomic*, **7**, 111–134.

Crick HQP, Dudley C, Glue DE, Thomson DL (1997) UK birds are laying eggs earlier. *Nature*, **388**, 526.

Crimmins TM, Crimmins MA, Bertelsen CD (2009) Flowering range changes across an elevation gradient in response to warming summer temperatures. *Global Change Biology*, **15**, 1141–1152.

Cross MS, Harte J (2007) Compensatory responses to loss of warming-sensitive plant species. *Ecology*, **88**, 740–748.

Cuming AC, Cho SH, Kamisugi Y, Graham H, Quatrano RS (2007) Microarray analysis of transcriptional responses to abcisic acid and osmotic, salt, and drought stress in the moss, Physcomitrella patens. *New Phytologist*, **176**, 275–287.

Dawes MA, Hagedorn F, Zumbrunn T, Handa T, Hättenschwiler S, Wipi S, Rixen C (2011) Growth and community responses of dwarf shrubs to in situ CO_2 enrichment and soil warming. *New Phytologist*, **191**, 806–818.

Day TA, Ruhland CT, Grobe CW, Xiong F (1999) Growth and reproduction of Antarctic vascular plants in response to warming and UV radiation reductions in the field. *Oecologia*, **119**, 24–35.

De Boeck HJ, Lemmens CMHM, Gielen B *et al.* (2007) Combined effects of climate warming and plant diversity loss on above- and below-ground grassland productivity. *Environmental and Experimental Botany*, **60**, 95–104.

De Boeck HJ, Lemmens CMHM, Zavalloni C *et al.* (2008) Biomass production in experimental grasslands of different species richness during three years of climate warming. *Biogeosciences*, **5**, 585–594.

De Frenne P, Brunet J, Shevtsova A *et al.* (2011) Temperature effects on forest herbs assessed by warming and transplant experiments along a latitudinal gradient. *Global Change Biology*, **17**, 3240–3253.

Devakumar AS, Prakash PG, Sathik MBM, Jacob J (1999) Drought alters the canopy architecture and micro-climate of Havea brasiliensis trees. *Trees*, **13**, 161–167.

Díaz P, Betti M, Sánchez DH, Udvardi MK, Monza J, Márquez AJ (2010) Deficiency in plastidic glutamine synthetase alters proline metabolism and transcriptomic response in *Lotus japonicus* under drouight stress. *New Phytologist*, **188**, 1001–1013.

Diemer M (2002) population stasis in a high-elevation herbaceous plant under moderate climate warming. *Basic and Applied Ecology*, **3**, 77–83.

van Doorslaer W, Stoks R, Jeppesen E, De Meester L (2007) Adaptive microevolutionary responses to simulated global warming in *Simocephalus vetelus*: a mesocosm study. *Global Change Biology*, **13**, 878–886.

Dorrepaal E, Aerts R, Cornelissen JHC, Callaghan TV, van Logtestijn RSP (2003) Summer warming and increased winter snow cover affect Sphagnum fuscum growth, structure and production in a sub-arctic bog. *Global Change Biology*, **10**, 93–104.

Dreesen FE, De Boeck HJ, Janssens I, Nijs I (2012) Summer heat and drought extremes trigger unexpected changes in productivity of a temperate annual/biannual plant community. *Environmetal and Experimental Botany*, **79**, 21–30.

Dubos C, Plomion C (2003) Identification of water-deficit responsive genes in maritime pine (*Pinus pinaster* Ait.) roots. *Plant Molecular Biology*, **51**, 249–262.

Dubos C, Le Povost G, Pot D *et al.* (2003) Identification and characterization of water-stress-responsive genes in hydroponically grown maritime pine (*Pinus pinaster*) seedlings. *Tree Physiology*, **23**, 169–179.

Durand TC, Sergeant K, Renaut J *et al.* (2011) Poplar under drought: comparison of leaf and cambial proteomic responses. *Journal of Proteomics*, **74**, 1396–1410.

Echevarría-Zomeño S, Ariza D, Jorge I, Lenz C, Del Campo A, Jorrin JV, Navarro RM (2009) Changes in the protein profile of *Quercus ilex* leaves in response to drought stress and recovery. *Journal of Plant Physiology*, **166**, 233–245.

Egli M, Hitz C, Fitze P, Mirabella A (2004) Experimental determination of climate-change effects on above-ground and below-ground organic matter in alpine grassland by translocation of soil cores. *Journal of Plant Nutrition and Soil Science*, **167**, 457–470.

Eichhorn MD, Fagan KC, Compton SG, Dent DH, Hertley SE (2007) Explaining leaf herbivory rates on tree seedlings in a Malasian rain forest. *Biotropica*, **39**, 416–421.

Elboutahiri N, Thami-Alami I, Udupa SM (2010) Phenotypic and genetic diversity in *Sinorhizobium meliloti* and *S. medicae* from drought and salt affected regions of Morocco. *BMC Microbiology.*, **10**, 15.

Elmendorf SC, Henry GHR, Hollister RD *et al*. (2012a) Plot-scale evidence of tundra vegetation change and links to recent summer warming. *Nature Climate Change*, **2**, 453–457.

Elmendorf SC, Henry GHR, Hollister RD *et al*. (2012b) Global assessment of experimental climate warming on tundra vegetation: heterogeneity over space and time. *Ecology Letters*, **15**, 164–175.

Elser JJ (2006) Biological stoichiometry: a chemical bridge between ecosystem ecology and evolutionary biology. *American Naturalist*, **168**, 525–535.

Elser JJ, Fagan WF, Denno RF *et al*. (2000) Nutritional constrains in terrestrial and freshwater food webs. *Nature*, **408**, 578–580.

Elser JJ, Andersen T, Baron JS *et al*. (2009) Shifts in lake N:P stoichiometry and nutrient limitation driven by atmospheric nitrogen deposition. *Science*, **326**, 835–836.

Endels P, Jacquemyn H, Brys R, Hermy M (2007) Genetic erosion explains deviation from demographic response to disturbance and year variation in relic population of perennial *Primula vulgaris*. *Journal of Ecology*, **95**, 960–972.

Erschbamer B (2007) Winners and losers of climate change in a central alpine glacier forelar. *Arctic Antartic and Alpine Research*, **39**, 237–244.

Erxleben A, Gewssler A, Vervliet-Scheebaum M, Reski R (2012) Metabolite profiling of the moss *Physcomitrella patens* reveals evolutionary conservation of osmoprotective substances. *Plant and Cell Reports*, **31**, 427–436.

Esmail S, Oelbermann M (2011) The impact of climate change on the growth of tropical agroforestry tree seedlings. *Agroforestry Systems*, **83**, 235–244.

Esquinas-Alcázar J (2005) Protecting crop genetic diversity for food security: political, ethical and technical challenges. *Nature Reviews Genetics*, **6**, 946–953.

Estiarte M, Filella I, Serra J, Peñuelas J (1994) Effects of nutrient and water stress on leaf phenolic content of peppers and susceptibility to generalist herbivore *Helicoverpa armigera* (Hubner). *Oecologia*, **99**, 387–391.

Estiarte M, Peñuelas J, Sardans J *et al*. (2008a) Root-surface phophatase activity in shrublands across a European gradient: effects of warming. *Journal of Environmental Biology*, **29**, 25–29.

Estiarte M, Peñuelas J, López-Martínez C, Pérez-Obiol R (2008b) Holocene palaeoenvironment in a former coastal lagoon of the arid south eastern Iberian Peninsula: salinization effects on δ15N. *Vegetation History and Archaeobotany*, **17**, 667–674.

Eveno E, Collada C, Guevara MA *et al*. (2008) “Contrasting patterns of selection at Pinus pinaster Ait. Drought stress candidate genes as revealed by genetic differentiation analyses. *Molecular Biology*, **25**, 417–437.

Fallour-Rubio D, Guibal F, Klein EK, Bariteau M, Leefévre F (2009) Rapid changes in plasticity across generations within an expanding cedar forest. *Journal of Evolution Biology*, **22**, 553–563.

Farnsworth EJ, Nuñez-Farfán J, Careaga SA, Bazzaz FA (1995) Phenology and growth of three temperate forest life forms in response to artificial soil warming. *Journal of Ecology*, **83**, 967–977.

Fay PA, Blair JM, Smith MD, Nipperi JB, Carlisle JD, Knapp AK (2011) Relative effects of precipitation variability and warming on tallgrass prairie ecosystem function. *Biogeosciences*, **8**, 3053–3068.

Feder ME, Blair N, Figueras H (1997) Natural thermal stress and heat-shock protein expression in Drosophilla larvae and pupae. *Functional Ecology*, **11**, 90–100.

Fensham RJ, Fairfax RJ, Ward DP (2009) Drought-induced tree death in savanna. *Global Change Biology*, **15**, 380–387.

Fernandez ME, Gyenge JE, de Urquiza MM, Varela S (2012) Adaptability to climate change in forestry species: drought effects on growth and wood anatomy of ponderosa pines growing at different competition levels. *Forest Systems*, **2**, 162–173.

Fernandes J, Morrow DJ, Casati P, Wallbot V (2008) Distinctive transcriptome response to adverse environmental conditions in *Zea mays* L. *Plant Biotechnology Journal*, **6**, 782–798.

Finzi AC, Austin AT, Cleland EE, Frey SD, Houlton BZ, Wallenstein MD (2011) Responses and feedbacks of coupled biogeochemical cycles to climate change: examples from terrestrial ecosystems. *Frontiers in Ecology and Environment*, **9**, 61–67.

Fisher EM, Seneviratne SI, Vidale PL, Luthi D, Schär C (2007) Soil moisture-atmosphere interactions during the 2003 European summer heat wave. *Journal of Climate*, **20**, 5081–5099.

Fitter AH, Fitter RSR (2002) Rapid changes in flowering time in British plants. *Science*, **296**, 1689–1691.

Fitzjarrald DR, Acevedo OC, Moore KE (2001) Climatic consequences of leaf presence in the eastern United States. *Journal of Climate*, **14**, 598–614.

Flexas J, Bota J, Loreto F, Cornic G, Sharkey TD (2004) Diffusive and metabolic limitations to photosynthesis under drought and salinity in C3 plants. *Plant Biology*, **6**, 269–279.

Foito A, Byrne SL, Shepherd T, Stewart D, Barth S (2009) Transcriptional and metabolic profiles of *Lolium perenne* L. genotypes in response to a PEG-induced water stress. *Plant Biotechnology Journal*, **7**, 719–732.

Forcada J, Trathan PN, Reid K, Murphy EJ, Croxall JP (2006) Contrasting population changes in sympatric penguin species in association with climate warming. *Global Change Biology*, **12**, 411–423.

Fordham DA, Akçakaya HR, Araújo MB *et al*. (2012) Plant extinction risk under climate change: are forecast range shifts alone a good indicator of species vulnerability to global change. *Global Change Biology*, **18**, 1357–1371.

Fox LR, Ribeiro SP, Brown VK, Masters GJ, Clarke IP (1999) Direct and indirect effects of climate change on St John's wort, *Hypericum perforatum* L. (Hypericaceae). *Oecologia*, **120**, 113–122.

Frank DA (2007) Drought effects on above- and belowground production of a grazed temperature grassland ecosystem. *Oecologia*, **152**, 131–139.

Frankenberg C, Butz A, Toon GC (2011) New global observations of the terrestrial carbon cycle from GOSAT: patterns of plant fluorescence with gross primary productivity. *Geophysical Research Letters*, **38**, L17706.

Frankham R (2005) Genetics and extinction. *Biologica Conservation*, **126**, 131–140.

Franks SJ, Sim S, Weis AE (2007) Rapid evolution of flowering time by an annual plant in response to a climate fluctuation. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 1278–1282.

Fridley JD (2012) Extended leaf phenology and the autumn niche in deciduous forest invasions. *Nature*, **485**, 359–362.

Fumagalli E, Baldoni E, Abbruscato P, Piffanelli P, Genga A, Lamanna R, Consonni R (2009) NMR techniques coupled with multivariate statistical analysis: tools to analyse *Oryza sativa* metabolic content under stress conditions. *Journal of Agronomy and Crop Science*, **195**, 77–88.

Gao S, Wang J, Zhang Z, Dong G, Guo J (2012) Seed production, mass, germinability, and subsequent seedling growth responses to parental warming environment in Leymus chinensis. *Crop and Pasture Science*, **63**, 87–94.

Garbulsky MF, Peñuelas J, Gamon J, Inoue Y, Filella I (2011) The photochemical reflectance index (PRI) and the remote sensing of leaf, canopy and ecosystem radiation use efficiencies. A review and meta-analysis. *Remote Sensing of Environment*, **115**, 281–297.

Garcia C, Hernandez T, Costa F (1994) Microbial activity in soils under Mediterranean environmental conditions. *Soil Biology and Biochemistry*, **26**, 1185–1191.

Gebler A, Keitel C, Kreuzwieser J, Matsysek R, Seiler W, Rennenberg H (2007) Potential risks for European beech (*Fagus sylvatica* L.) in a changing climate. *Trees*, **21**, 1–11.

Gedan KB, Bertness MD (2009) Experimental warming causes rapid loss of plant diversity in New England salt marshes. *Ecology Letters*, **12**, 842–848.

Gienapp P, Teplitsky C, Alho JS, Mills A, Merilä J (2008) Climate change and evolution: disentangling environmental and genetic responses. *Molecular Ecology*, **17**, 167–178.

Giménez-Benavides L, García-Camacho R, Iriondo JM, Escudero A (2011) Selection on flowering time in Mediterranean high-mountain plants under global warming. *Evolution Ecology*, **25**, 777–794.

Ginzberg I, Barel G, Ophir R *et al*. (2009) Transcriptomic profiling of heat-stress response in potato periderm. *Journal of Experimental Botany*, **60**, 4411–4421.

Godfree R, Lepschi B, Reside A, Bolgers T, Roberstson B, Marshall D, Carnegie M (2011) Multiscale topoedaphic heterogeneity increases resilence and resistance of a dominant grassland species to extreme drought and climate change. *Global Change Biology*, **17**, 943–958.

Gordon C, Woodin SJ, Mullins CE, Alexander IJ (1999a) Effects of environmental change, including drought, on water use by competing *Calluna vulgaris* (heather) and *Pteridium aquilinum* (bracken). *Functional Ecology*, **13** (Suppl. 1), 96–106.

Gordon C, Woodin SJ, Alexander IJ, Mullins CE (1999b) Effects of increased temperature, drought and nitrogen supply on two upland perennials of contrasting functional type: *Calluna vulgaris* and *Pteridium aquilinum*. *New Phytologist*, **142**, 243–258.

Gornall JL, Woodin SJ, Jonsdóttir IS, Van der Wal R (2009) Herbivore impacts to the moss layer determine tundra ecosystem response to grazing and warming. *Oecologia*, **161**, 747–758.

Green K (2010) Alpine taxa exhibit responses to climate warming in the snowy Mountains of Australia. *Journal of Mountain Science*, **2**, 167–175.

Gunderson CA, O'Hara KH, Campion CM, Walker AV, Edwards NT (2010) Thermal plasticity of pjotosynthesis: the role of acclimation in forest responses to a warming climate. *Global Change Biology*, **16**, 2272–2286.

Guo K, Hao SG, Sun OJ, Kang L (2009) Differential responses to warming and increased precipitation among three contrasting grasshopper species. *Global Change Biology*, **15**, 2539–2548.

Gutbrodt B, Dorn S, Mody K (2012) Drought stress affects constitutive but not induced herbivore resistance in apple plants. *Arthropod-Plant Interactions*, **6**, 171–179.

Gutschick VP, BassiriRad H (2003) Extreme events as shaping physiology, ecology, and evolution of plants: towards a unified definition and evaluation of their consequences. *New Physiology*, **160**, 21–42.

Guy C, Kaplan F, Kopka J, Selbig J, Hincha DK (2008) Metabolomics of temperature stress. *Physiology Plantarum*, **132**, 220–235.

Hale BK, Herms DA, Hansen RC, Clausen TP, Arnold D (2005) Effects of drought stress and nutrient availability on dry matter allocation, phenolic glycosides, and rapid induced resistance of poplar to two Lymantrid defoliators. *Journal of Chemical Ecology*, **31**, 2601–2620.

Hamanishi ET, Campbell MM (2011) Genome-wide responses to drought in forest trees. *Forestry*, **84**, 273–283.

Hamanishi ET, Raj S, Wilkins O, Thomas BR, Mansfield SD, Plant AL, Campbell MM (2010) Intraspecific variation in the *Populus balsamifera* drought transcriptome. *Plant Cell and Environment*, **33**, 1742–1755.

Hampe A, Jump AS (2011) Climate relicts: past, present and future. *Annual Reviews of Ecology Evolution and Systematics*, **42**, 313–333.

Harada T, Nitta S, Ito K (2005) Photoperiodic changes according in global warming in wing-form determination and diapauses induction of a water strider, *Aquarius paludum* (Heteroptera: Gerridae). *Applied Entomology and Zoology*, **40**, 461–466.

Harrison S, Damschen EI, Grace JB (2010) Ecological contingency in the effects of climatic warming on forest herb communities. *Proceedings of the National Academy of Sciences of the United States of America*, **107**, 19362–19367.

Hartley AE, Neill C, Melillo JM, Crabtree R, Bowles FP (1999) Plant performance and soil nitrogen mineralization in response to simulated climate change in subartic dwarf shrub heath. *Oikos*, **86**, 331–343.

Haugen R, Steffes L, Wolf J, Brown P, Matzner S, Siemens DH (2008) Evolution of drought tolerance and defense: dependence of tradeoffs on mechanism, environment and defense switching. *Oikos*, **117**, 231–244.

He JS, Zhang QB, Bazzaz EA (2005) Differential drought responses between saplings and adult trees in four co-occuring species of New England. *Trees*, **19**, 442–450.

He CY, Zhang JG, Duan AG, Sun HG, Fu LH, Zheng SX (2007) Proteins responding to drought and high-temperature stress in *Pinus armandii* Franch. *Canadian Journal of Botany*, **85**, 994–1001.

He C, Zhang J, Duan A, Zheng S, Sun H, Fu L (2008) Proteins responding to drought and high-temperature stress in *Populus* x *euramerica* cv. '74/76. *Trees*, **22**, 803–813.

He WM, Li JJ, Peng PH (2012) A congeneric comparison shows that experimental warming enhances the growth of invasive Eupatorium adenophorum. *PLoS ONE*, **7**, e35681.

Heath LS, Ramakrishnan N, Sederoff RR *et al.* (2002) Studying the functional genomics of stress responses in loblolly pine with the expresso microarray experiment management system. *Comparative and Functional Genomics*, **3**, 226–243.

Heckathorn SA, DeLucia EH (1994) Drought-onduced nitrogen retranslocation in perennial C4 grasses of tallgrass praire. *Ecology*, **75**, 1877–1886.

Hedhly A, Hormaza JI, Herrero M (2008) Global warming and sexual plant reproduction. *Trends in Plant Science*, **14**, 30–36.

Henry GHR, Molau U (1997) Tundra plants and climate change: the international tundra experiment (ITEX). *Global Change Biology*, **3** (Suppl. 1), 1–9.

Hill CB, Henry GHR (2011) Responses of high Artic wet sedge tundra to climate warming since 1980. *Global Change Biology*, **17**, 276–287.

Hobbie SE, Chapin FS (1996) Winter regulation of tundra litter carbon and nitrogen dynamics. *Biogeochemistry*, **35**, 327–338.

Hobbie SE, Shevtsova A, Chapin FS (1999) Plant responses to species removal and experimental warming in Alaskan tussock tundra. *Oikos*, **84**, 417–434.

Hoeppner SS, Dukes JS (2012) Interactive responses of old-field growth and composition to warming and precipitation. *Global Change Biology*, **18**, 1754–1768.

Hoffmann AA, Sgrò CM (2011) Climate change and evolutionary adaptation. *Nature*, **470**, 479–485.

Hoffmann AA, Willi Y (2008) Detecting genetic responses to environmental change. *Nature Reviews Genetics*, **2**, 421–432.

Hofgaard A, Lokken JO, Dalen L, Hytteborn H (2010) Comparing warming and grazing effects on birch growth in an alpine environment – a 10-year experiment. *Plant Ecology and Diversity*, **3**, 19–27.

Hollister RD, Flaherty KJ (2010) Above- and below-ground biomass response to experimental warming in northern Alaska. *Applied Vegetation Science*, **13**, 378–387.

Hollister RD, Webber PJ, Tweed GE (2005) The response of Alaskan arctic tundra to experimental warming: differences between short- and long-term responses. *Global Change Biology*, **11**, 525–536.

Hong Y, Zheng S, Wang X (2008) Dual functions of phospholipase D 1 in plant response to drought. *Molecular Plant*, **1**, 262–269.

Hoover SER, Ladley JJ, Shchepetkina AA, Tisch M, Gieseg SP, Tylianakis JM (2012) Warming, CO_2, and nitrogen deposition interactively affect a plant-pollinator mutualism. *Ecology Letters*, **15**, 227–234.

Hovenden MJ, Wills KE, Schoor JKV, Chaplin RE, Williams AL, Nolan MJ, Newton PCD (2007) Flowering, seed production and seed mass in a species-rich temperate grassland exposed to FACE and warming. *Australian Journal of Botany*, **55**, 780–794.

Huelber K, Gottfried M, Pauli H, Reiter K, Winkler M, Grabherr G (2006) Phenological responses of snowbed species to snow removal dates in the Central Alps: implications for climate warming. *Artic, Antartic and Alpine Research*, **38**, 99–103.

Huntley B (1991) How plants respond to climate change: migration rates, individualism and the consequences for plant communities. *Annals of Botany*, **67** (Suppl.), 15–22.

Hutchison JS, Henry HAL (2010) Additive effects of warming and increased nitrogen deposition in a temperate old field: plant productivity and the importance of winter. *Ecosystems*, **13**, 661–672.

Inclan R, Gimeno BS, Dizengremel P, Sanchez M (2005) Compensation processes of Aleppo pine (*Pinus halepensis* Mill.) to ozone exposure and drought stress. *Environmental Pollution*, **137**, 517–524.

IPCC (2007) Climate Change 2007: The physical science basis. In: *Contribution of Working Group I to the Fourth Assessment Report of the Intergovernmental Panel on Climate Change* (eds Solomon S, Qin D, Manning M, Chen Z, Marquis M, Averyt KB, Tignor M, Miller HL). Cambridge University Press, Cambridge, New York, NY.

Iszkulo G, Jasinska AK, Giertych MJ, Boratynski A (2009) Do secondary sexual dimorphism and female intolerance to drought influence the sex ratio and extinction risk of *Taxus baccata*? *Plant Ecology*, **200**, 229–240.

Jarrad FC, Wahren CH, Williams RJ, Bugman MA (2009) Subalpine plants show short-term positive growth responses to experimental warming and fire. *Australian Journal of Botany*, **57**, 465–473.

Jay F, Manel S, Alvarez N *et al.* (2012) Forecasting changes in population genetic structure of alpine plants in response to global warming. *Molecular Ecology*, **21**, 2354–2368.

Jentsch A, Kreyling J, Boettcher-Treschkov J, Beierkuhnlein C (2009) Beyond gradual warming: extreme weather events alter flower phenology of European grassland and heath species. *Global Change Biology*, **15**, 837–849.

Jiang X, Niu GY, Yang ZL (2009) Impacts of vegetation and groundwater dynamics on warm season precipitation over the central United States. *Journal of Geophysical Research*, **114**, D06109.

Jiang T, Fountain J, Davis G, Kemerait R, Scully B, Lee RD, Guo B (2012) Root morphology and gene expression analysis in response to drought stress in maize (*Zea mays*). *Plant Molecular Biology Reports*, **30**, 360–369.

Joly K, Jandt RR, Klein DR (2009) Decrease of lichens in Arctic ecosystems: the role of wildfire, caribou, reindeer, competition and climate in north-western Alaska. *Polar Research*, **28**, 433–442.

Jónsdóttir IS, Khitun O, Stenstrom A (2005a) Biomass and nutrient responses of a clonal tundra sedge to climate warming. *Canadian Journal of Botany*, **83**, 1608–1621.

Jónsdóttir IS, Magnússon B, Gudmundsson I, Elmarsdóttir A, Hjartarson H (2005b) Variable sensitivity of plant communities in Iceland to experimental warming. *Global Change Biology*, **11**, 553–563.

Jönsson AM, Appelberg G, Harding S, Barring L (2009) Spatio-temporal impact of climate change on the activity and voltinism of the spruce bark beetle, *Ips typographus*. *Global Change Biology*, **15**, 486–499.

Jump AS, Peñuelas J (2005) Running to stand still: adaptation and the response of plants to rapid climate change. *Ecology Letters*, **8**, 1010–1020.

Jump AS, Peñuelas J (2006) Genetic effects of chronic habitat fragmentation in a wind-pollinated tree. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 8096–8100.

Jump AS, Hunt JM, Martínez-Izquierdo JA, Peñuelas J (2006a) Natural selection and climate change: temperature-linked apatial and temporal trends in gene frequency in *Fagus sylvatica*. *Molecular Ecology*, **15**, 3469–3480.

Jump AS, Hunt JM, Peñuelas J (2006b) Rapid climate change-related growth decline at the southern range edge of *Fagus sylvatica*. *Global Change Biology*, **12**, 2163–2174.

Jump AS, Hunt JM, Peñuelas J (2007) Climate relationships of growth and establishment across the altitudinal range of *Fagus sylvatica* in the Montseny Mountains, northeast Spain. *Ecoscience*, **14**, 507–518.

Jump AS, Peñuelas J, Rico L, Ramallo E, Estiarte M, Martínez-Izquierdo JA, Lloret F (2008) Simulated climate change provokes rapid genetic change in the Mediterranean shrub *Fumana thymifolia*. *Global Change Biology*, **14**, 637–643.

Jump AS, Mátyás C, Peñuelas J (2009a) The altitude-for-latitude disparity in the range retractions of woody species. *Trends in Ecology and Evolution*, **24**, 694–701.

Jump AS, Marchant R, Peñuelas J (2009b) Environmental change and the option value of genetic diversity. *Trends in Plant Science*, **14**, 51–58.

Jyske T, Holtta T, Makinen H, Noid P, Lumme I, Spiecker H (2010) The effect of artificially induced drought on radial increment and wood properties of Norway spruce. *Tree Physiology*, **30**, 103–115.

Kaplan F, Kopka J, Haskell DW *et al.* (2004) Exploring the temperature-stress metabolome of *Arabidopsis*. *Plant Physiology*, **136**, 4159–4168.

Kardol P, Campany CE, Souza L, Norby RJ, Weltzin JF, Classen AT (2010) Climate change effects on plant biomass alter dominance patterns and community composition evenness in a experimental old-field ecosystem. *Global Change Biology*, **16**, 2676–2687.

Karrenberg S, Widmer A (2008) Ecological relevant genetic variation from a non-*Arabidopsis* perspective. *Current Opinion in Plant Biology*, **11**, 156–162.

Kattge J, Díaz S, Lavorel S *et al.* (2011) TRY – a global database of plant traits. *Global Change Biology*, **17**, 2905–2935.

Kearney M, Shine R, Porter WP (2009) The potential for behavioral thermoregulation to buffer “cold-blooded” animals against climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **106**, 3835–3840.

Klanderud K, Totland O (2007) The relative role of dispersal and local interactions for alpine plant community diversity under simulated climate warming. *Oikos*, **116**, 1279–1288.

Klein JA, Harte J, Zhao XQ (2004) Experimental warming causes large and rapid species loss, dampened by simulated grazing, on the Tibetan Plateau. *Ecology Letters*, **7**, 1170–1179.

Kocsis M, Hufnagel L (2011) Impacts of climate change on Lepidoptera species and communities. *Applied Ecology and Environmental Research*, **9**, 43–72.

Kongstad J, Schmidt IK, Riis-Nielsen T, Arndal MF, Mikkelsen TN, Beier C (2012) High resilence in heathland plants to changes in temperature, drought, and CO_2 in combination: results from the CLIMAITE experiment. *Ecosystems*, **15**, 269–283.

Körner C (1995) Towards a better experimental basis for upscaling plant responses to elevated CO_2 and climate warming. *Plant Cell and Environment*, **18**, 1101–1110.

Körner C (2007) The use of “altitude” in ecological research. *Trends in Ecology and Evolution*, **22**, 569–574.

Krugman T, Peleg Z, Quansah L *et al.* (2011) Alteration in expression of hormone-related genes in wild emmer wheat roots associated with drought adaptation mechanisms. *Functional Integrative Genomics*, **11**, 565–583.

Kudo G, Suzuki S (2003) Warming effects on growth, production, and vegetation atructure of alpine shrubs: a five-year experiment in northern Japan. *Oecologia*, **135**, 280–287.

Kullman L (2008) Thermophilic tree species reinvade subalpine Sweden-early responses to anomalous late Holocene climate warming. *Artic Antartic and Alpine Research*, **40**, 104–110.

La Sorte FA, Jetz W (2010) Projected range concentrations of montane biodiversity under global warming. *Proceedings of the Royal Society B*, **277**, 3401–3410.

Laaksonen A, Kulmala M, O’Dowd CD *et al.* (2008) The role of VOC oxidation products in continental new particle formation. *Atmospheric Chemistry and Physics*, **8**, 2657–2665.

Legnaioli T, Cuevas J, Mas P (2009) TOC1 functions as a molecular switch connecting the circadian clock with plant responses to drought. *The EMBO Journal*, **28**, 3745–3757.

Lambrecht SC, Loik ME, Inoure DW, Harte J (2006) Reproductive and physiological responses to simulated climate warming for four subalpine species. *New Phytologist*, **173**, 121–134.

Lang SI, Cornelissen JHC, Shaver GR *et al.* (2012a) Arctic warming on two continents has consistent negative effects in lichen diversity and mixed effects on bryophyte diversity. *Global Change Biology*, **18**, 1096–1107.

Lang B, Rall BC, Brose U (2012b) Warming effects on consumption and intraspecific interference competition depend on predator metabolism. *Journal of Animal Ecology*, **81**, 516–523.

Larkindale J, Huang BR (2004) Changes of lipid composition and saturation level in leaves and roots for heat-stressed and heat-acclimated creeping bentgrass (*Agrostis stolonifera*). *Environmental and Experimental Botany*, **51**, 57–67.

Leimu R, Mutikainen P, Koricheva J, Fischer M (2006) How general are positive relationships between plant population size, fitness and genetic variation? *Journal of Ecology*, **94**, 942–952.

Lenoir J, Gégout JC, Guisan A *et al.* (2010) Going against the flow: potential mechanisms for unexpected downslope range shifts in a warming climate. *Ecography*, **33**, 295–303.

Lepetz V, Massot M, Chaine AS, Clobert J (2009) Climate warming and the evolution of morphotypes in a reptile. *Global Change Biology*, **15**, 454–466.

Leuzinger S, Luo YQ, Beier C, Dieleman W, Vicca S, Korner C (2011) Do global change experiments overstimate impacts on terrestrial ecosystems?. *Trends in Ecology & Evolution*, **26**, 236–241.

Li C, Han LB (2012) Enhanced drought tolerance of tobacco overexpressing OJERF gene is associated with alteration in proline and antioxidant metabolism. *Journal of the American Society for Horticultural Science*, **137**, 107–113.

Li WX, Oono Y, Zhu J *et al.* (2008a) The Arabidopsis NFYA5 transcription factor is regulated transcriptionally and posttranscriptionally to promote drought resistance. *The Plant Cell*, **20**, 2238–2251.

Li B, Wei A, Song C, Li N, Zhang J (2008b) Heterologous expression of the TsVP gene improves the drought resistance in maize. *Plant Biotechnology Journal*, **6**, 146–159.

Li N, Wang GX, Gao YH, Wang JF (2011a) Warming effects on plant growth, soil nutrients, microbial biomass and soil enzymes activities of two alpine meadows in Tibetan plateau. *Polish Journal of Ecology*, **59**, 25–35.

Li G, Liu Y, Frelich LE, Sun S (2011b) Experimental warming induces degradation of a Tibetan alpine meadow through trophic interactions. *Journal of Applied Ecology*, **48**, 659–667.

Li XY, Contreras S, Solé-Benet A *et al.* (2011d) Controls of infiltration-runoff processes in Mediterranean karst rangelands in SE Spain. *Catena*, **86**, 98–109.

Liancourt P, Spence LA, Boldgiv B, Lkhagva A, Helliker BR, Casper BB, Petraitis PS (2012) Vulnerability of the northern Mongolian steppe to climate change: insights from flower production and phenology. *Ecology*, **93**, 815–824.

Linares JC, Camarero JJ (2012) From pattern to process: linking intrinsic water-use efficiency to drought-induced forest decline. *Global Change Biology*, **18**, 1000–1015.

Liu S, Jiang Y (2010) Identification of differentially expressed genes under drought stress in perennial ryegrass. *Physiologia Plantarum*, **139**, 375–387.

Liu Y, Mu J, Niklas KJ, Li G, Sun S (2012) Global warming reduces plant reproductive output for temperate multi-inflorescence species on the Tibetan plateau. *New Phytologist*, **195**, 427–436.

Llorens L, Peñuelas J (2005) Experimental evidence of future drier and warmer conditions affecting flowering of two co-occuring Mediterranean shrubs. *International Journal of Plant Science*, **166**, 235–245.

Llorens L, Peñuelas J, Estiarte M (2003) Ecophysiological responses of two Mediterranean shrubs, *Erica multiflora* and *Globularia alypum*, to experimentally drier and warmer conditions. *Physiologia Plantarum*, **119**, 231–243.

Lloret F, Peñuelas J, Ogaya R (2004a) Establishment of co-occuring Mediterranean tree species under a varying soil moisture regime. *Journal of Vegetation Science*, **15**, 237–244.

Lloret F, Peñuelas J, Estiarte M (2004b) Experimental evidence of reduced diversity of seedlings doe to climate modification in a Mediterranean-type community. *Global Change Biology*, **10**, 248–258.

Lloret F, Peñuelas J, Prieto P, Llorens L, Estiarte M (2009) Plant community changes induced by experimental climate change: seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics*, **11**, 53–63.

Llusia J, Peñuelas J, Ogaya R, Alessio G (2010) Annual and seasonal changes in foliar terpene content and emission rates in Cistus albidus L. Submitted to soil drought in Prades forest (Catalonia, NE Spain). *Acta Physiologica Plantarum*, **32**, 387–394.

Llusia J, Peñuelas J, Alessio GA, Ogaya R (2011) Species-specific, seasonal, interannual, and historically-accumulated changes in foliar terpene emission rates in *Phillyrea latifolia* and *Quercus ilex* submitted to rain exclusion in the Prades Mountains (Catalonia). *Russian Journal of Plant Physiology*, **58**, 126–132.

Loe LE, Bonenfant C, Mysterud A *et al.* (2005) Climate predictability and breeding phenology in red deer: timing and synchrony of rutting and calving in Norway and France. *Journal of Animal Ecology*, **74**, 579–588.

Lorenz WW, Sun F, Liang C *et al.* (2005) Water stress-responsive genes in loblolly pine (*Pinus taeda*) roots identified by analyses of expressed sequence tag libraries. *Tree Physiology*, **26**, 1–16.

Lowe RGT, Lord M, Rybak K, Trengove RD, Oliver RP, Solomon PS (2008) A metabolomic approach to dissecting osmotic stress in the wheat pathogen *Stagonospora nodorum*. *Fungal Genetics and Biology*, **45**, 1479–1486.

Lugan R, Niogret MF, Kervazo L, Larher FR, Kopka J, Bouchereau A (2009) Metabolome and water status phenotyping of *Arabidopsis* under abiotic stress cues reveals new insight into ESK1 function. *Plant Cell and Environment*, **32**, 95–108.

Luikart G, England PR, Tallmon D, Jordan J, Taberlet P (2003) The power and promise of population genomics: from genotyping to genome typing. *Nature Reviews Genetics*, **4**, 981–994.

Ma G, Ma CS (2012) Effect of acclimation on heat-escape temperatures of two aphid species: implications for estimating behavioral response of insects to climate warming. *Journal of Insect Physiology*, **58**, 303–309.

Malcolm JB, Liu C, Neilson RP, Hansen L (2005) Global warming and extinctions of endemic species from biodiversity hotspots. *Conservation Biology*, **20**, 538–548.

Malmendal A, Overgaard J, Bundy JG, Sarensen JG, Nielsen NC, Loescheke V, Holmstrup M (2006) Metabolomic profiling of heat stress: handering and recovery of homeostasis in *Drosophila*. *American Journal of Physiology Regulation and Integrative Comparative Physiology*, **291**, R205–R215.

Mane SP, Vázquez Robinet C, Ulanov A *et al.* (2008) Molecular and Physiological adaptation to prolonged drought stress in the leaves of two Andean patato Genotype. *Functional Plant Biology*, **35**, 669–688.

Marchin R, Zeng HN, Hoffmann W (2010) Drought-deciduous behavior reduces nutrient losses from temperate deciduous trees under severe drought. *Oecologia*, **163**, 845–854.

Martin TE, Maron JL (2012) Climate impacts on bird and plant communities from altered animal-plant interactions. *Nature Climate Change*, **2**, 195–200.

Mátyás C, Nagy E, Ujvári J (2008) Genetic background of response of trees to aridificacion at the xeric forest limit and consequences for bioclimatic modeling. In: *Bioclimatology and Natural Hazards* (eds Strelcová K, Mátyás C, Kleidon A, Lapin M, Matejka F, Blazenec M, Åkvarenina J, Holecy J), pp. 179–196. Springer Verlag, Berlin, Germany.

Meier IC, Leuschner C (2008) Belowground drought response of European beech: fine root biomass and carbon partitioning in 14 mature stands across a precipitation gradient. *Global Change Biology*, **14**, 2081–2095.

Meiri D, Breiman A (2009) Arabidopsis ROF1 (FKBP62) modulates thermotolerance by interacting with HSP90.1 and affecting the accumulation of HsfA2-regulated sHSPs. *The Plant Journal*, **59**, 387–399.

Memmott J, Graze PG, Waser NM, Price MV (2007) Global warming and the disruption of plant-pollinator interactions. *Ecology Letters*, **10**, 710–717.

Menzel A, Fabian P (1999) Growing season extended in Europe. *Nature*, **397**, 659.

Menzel A, Sparks TH, Estrella N *et al.* (2006) European phonological response to climate change matches the warming pattern. *Global Change Biology*, **12**, 1069–1976.

Messaoud Y, Chen YH (2011) The influence of recent climate change on tree height growth differs with species and spatial environment. *PLoS ONE*, **6**, e14691.

Michaud MR, Benoit JB, López-Martínez G, Elnitsky MA, Lee RE Jr, Denlinger DL (2008) Metabolomics reveals unique and shared metabolic changes in response to heat shock, freezing and desiccation in the Atlantic midge. *Journal of Insect Physiology*, **54**, 645–655.

Michelsen A, Jonasson S, Sleep D, Havström M, Callaghan TV (1996) Shoot biomass, d13C, nitrogen and chlorophyll responses of two artic dwarf shrubs to in situ shading, nutrient application and warming simulating climate change. *Oecologia*, **109**, 1–12.

Molau U (1997) Responses to natural climatic variation and experimental warming in two tundra plant species with contrasting life forms: *Cassiope tetragona* and *Ranunculus nivalis*. *Global Change Biology*, **3** (Suppl. 1), 97–107.

Molgaard P, Christensen K (1997) Response to experimental warming in a population of Papaver radicatum in Greenland. *Global Change Biology*, **3** (Suppl. 1), 116–124.

Molina-Montenegro MA, Quiroz CI, Torres-Díaz C, Atala C (2011) Functional differences in response to drought in the invasive *Taraxacum officinale* from native and introduced alpine habitat ranges. *Plant Ecology and Diversity*, **4**, 37–44.

Mora CL, Driese SG, Colarusso LA (1996) Middle to late Paleozoic atmosphere CO2 levels from soil carbonate and organic matter. *Science*, **271**, 1105–1107.

Moreno-Gutiérrez C, Battipaglia G, Cherubini P, Saurer M, Nicolás E, Contreras S, Querejeta JI (2012) Stand structure modulates the long-term vulnerability of *Pinus halepensis* to climatic drought in a semiarid Mediterranean ecosystem. *Plant Cell and Environment*, **35**, 1026–1039.

Muhammad Ali G, Komatsu S (2006) Proteomic analysis of rice leaf sheath during drought stress. *Journal of Proteome Research*, **5**, 396–403.

Munier A, Hermanutz L, Jacobs JD, Lewis K (2010) The interacting effects of temperature, ground disturbance, and herbivory on seedling establishment: implications for treeline advance with climate warming. *Plant Ecology*, **210**, 19–30.

Na L, Genxu W, Yan Y, Yongheng G, Guangsheng L (2011) Plant production, and carbon and nitrogen source pools, are strongly intensified by experimental warming in alpine ecosystems in the Qinghai-Tibet Plateau. *Soil Biology & Biochemistry*, **43**, 942–953.

Natali SM, Schuur EAG, Rubin RL (2012) Increased plant productivity in Alaskan tundra as a result of experimental warming of soil and permafrost. *Journal of Ecology*, **100**, 488–498.

Naya L, Ladrera R, Ramos J, González EM, Arrese-Igor MF, Becana M (2007) The response of carbón metabolism and antioxidant defenses of alfalfa nodules to drought stress and to the subsequent recovery of plants. *Plant Physiology*, **144**, 1104–1114.

Neven LG (2000) Physiological response of insects to heat. *Postharvest Biology and Technology*, **21**, 103–111.

Neven LG, Rehfield LM (1995) Comparison of Prestorage heat treatments on fifth-instar coding moth (Lepidoptera: Tortricidae) mortality. *Journal of Economic Entomology*, **88**, 1371–1375.

Newman D, Pilson D (1997) Increased probability of extinction due to decreased genetic effective population size: experimental populations of *Clarkia pulchella*. *Evolution*, **51**, 354–362.

Nguyen TTA, Michaud D, Cloutier C (2009) A proteomic analysis of the aphid *Macrosiphum euphorbiae* under heat and radiation stress. *Insect and Molecular Biology*, **39**, 20–30.

Nijs I, Teuchels H, Blum H, Hendrey G, Impens I (1996) Simulation of climate change with infrared heaters reduces the productivity of *Lolium perenne* L. in summer. *Environmental and Experimental Botany*, **36**, 271–280.

Ning J, Li X, Hicks LM, Xiong L (2010) A raf-like MAPKKK gene DSM1 mediates drought resistance through reactive oxygen species scavenging in rice. *Plant physiology*, **152**, 876–890.

Nybakken L, Sandvik SM, Klanderud K (2011) Experimental warming had little effect on carbon-based secondary compounds, carbon and nitrogen in selected alpine plants and lichens. *Environmental and Experimental Botany*, **72**, 368–376.

Ogaya R, Peñuelas J (2003) Comparative field study of *Quercus ilex* and *Phillyrea latifolia* photosynthetic response to experimental drought conditions. *Environmental and Experimental Botany*, **50**, 137–148.

Ogaya R, Peñuelas J (2004) Phenological patterns of *Quercus ilex*, *Phillyrea latifolia*, and *Arbutus unedo* growing under a field experimental drought. *Écoscience*, **11**, 263–270.

Ogaya R, Peñuelas J (2005) Decreased mushroom production in a holm oak forest in response to an experimental drought. *Forestry*, **78**, 279–283.

Ogaya R, Peñuelas J (2006) Contrasting foliar responses to drought in *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum*, **50**, 373–382.

Ogaya R, Peñuelas J (2007a) Tree growth, mortality, and above-ground biomass accumulation in a holm oak forest under a five-year experimental field drought. *Plant Ecology*, **189**, 291–299.

Ogaya R, Peñuelas J (2007b) Species-specific drought effects on flower and fruit production in a Mediterranean holm oak forest. *Forestry*, **180**, 351–357.

Ogaya R, Peñuelas J, Asensio D, Llusia J (2011) Chlorophyll fluorescence responses to temperature and water availability in two co-dominant Mediterranean shrub and tree species in a long-term field experiment simulating climate change. *Environmental and Experimental Botany*, **73**, 89–93.

Oh SJ, Kim YS, Kwon CW, Park HK, Jeong JS, Kim JK (2009) Overexpression of the transcription factor AP37 in rice improves grain yield under drought conditions. *Plant Physiology*, **150**, 1368–1379.

Olsrud M, Carlsson BA, Svensson BM, Michelsen A, Melillo JM (2010) Responses of fungal root colonization, plant cover and leaf nutrients to long-term exposure to elevated atmospheric CO2 and warming in a subartic birch forest understory. *Global Change Biology*, **16**, 1820–1829.

Ozgul A, Childs DZ, Oli MK *et al.* (2010) Coupled dynamics of body mass and population growth in response to environmental change. *Nature*, **466**, 482–485.

Padmalatha KV, Dhandapani G, Kanakachari M *et al.* (2012) Genome-wide transcriptomic analysis of cotton under drought stress reveal significant down-regulation of genes and pathways involved in fibre elongation and up-regulation of defense responsive genes. *Plant Molecular Biology*, **78**, 223–246.

Parida AK, Dagaonkar VS, Phalak MS, Umalkar GV, Aurangabadkar LP (2007) Alterations in photosynthetic pigments, protein and osmotic components in cotton genotypes subjected to short-term drought stress followed by recovery. *Plant Biotechnology*, **1**, 37–48.

Parmesan C, Yohe G (2003) A globally coherent fingerprinting of climate change impacts scross natural systems. *Nature*, **421**, 37–42.

Parmesan C, Ryrholm N, Stefanescu C *et al.* (1999) Poleward shifts in geographical ranges of butterfly species associated with regional warming. *Nature*, **399**, 579–583.

Parolin P, Lucas C, Piedade MTF, Wittmann F (2010) Drought responses of flood-tolerant trees in Amazonian floodplains. *Annals of Botany*, **105**, 129–139.

van Peer L, Nijs I, Reheul D, De Cauwer B (2004) Species richness and susceptibility to heat and drought extremes in synthesized grassland ecosystems: compositional vs physiological effects. *Functional Ecology*, **18**, 769–778.

Peña-Rojas K, Aranda X, Jofre R, Fleck I (2006) Leaf mosphology, photochemistry and water status changes in resprouting *Quercus ilex* under drought. *Functional Plant Biology*, **32**, 117–130.

Peng C, Ma Z, Lei X *et al.* (2011) A drought-induced pervasive increase in tree mortality across Canada's boreal forest. *Nature Climate Change*, **1**, 467–471.

Peñuelas J, Boada M (2003) A global change-induced biome shift in the Montseny mountains (NE Spain). *Global Change Biology*, **9**, 131–140.

Peñuelas J, Filella I (2001) Responses to a warming world. *Science*, **294**, 793–794.

Peñuelas J, Llusia J (2003) BVOCs: plant defense against climate warming? *Trends in Plant Science*, **8**, 105–109.

Peñuelas J, Sardans J (2009) Elementary factors. *Nature*, **460**, 803–804.

Peñuelas J, Staudt M (2010) BVOCs and global change. *Trends in Plant Science*, **15**, 133–144.

Peñuelas J, Biel C, Estiarte M (1993) Changes in biomass, chlorophyll content and gas exchange of beans and peppers under nitrogen and water stress. *Photosynthetica*, **29**, 535–542.

Peñuelas J, Filella I, Llusia J, Siscart D, Piñol J (1998) Comparative field study of spring and summer leaf gas exchange and photobiology of the mediterranean trees *Quercus ilex* and *Phillyrea latifolia*. *Journal Experimental Botany*, **49**, 229–238.

Peñuelas J, Filella I, Lloret F, Piñol J, Siscart D (2000a) Effects of a severe drought on water and nitrogen use by *Quercus ilex* and *Phillyrea latifolia*. *Biologia Plantarum*, **43**, 47–53.

Peñuelas J, Lloret F, Montoya R (2000b) Several drought effects on Mediterranean woody flora in Spain. *Forest Science*, **47**, 214–218.

Peñuelas J, Filella I, Comas P (2002) Changed plant and animal life cycles from 1952–2000 in the Mediterranean region. *Global Change Biology*, **8**, 531–544.

Peñuelas J, Gordon C, Llorens L *et al*. (2004a) Nonintrusive field experiments show different plant responses to warming and drought among sites, seasons, and species in a North-South European gradient. *Ecosystems*, **7**, 598–612.

Peñuelas J, Filella I, Zhang X *et al*. (2004b) Complex spatiotemporal phonological shifts as a response to rainfall changes. *New Phytologist*, **161**, 837–846.

Peñuelas J, Llusia J, Asensio D, Munné-Bosch S (2005) Linking isoprene with thermotolerance, antioxidants and monoterpene emissions. *Plant Cell and Environment*, **28**, 278–286.

Peñuelas J, Ogaya R, Boada M, Jump AS (2007a) Migration, invasion and decline: changes in recruitment and forest structure in a warming-linked shift of European beech forest in Catalonia (NE Spain). *Ecography*, **30**, 829–837.

Peñuelas J, Prieto P, Beier C *et al*. (2007b) Response of plant species richness and primary productivity in shrublands along a north-south gradient in Europe to seven years of experimental warming and drought: reductions in primary productivity in the heat and drought year of 2003. *Global Change Biology*, **13**, 2563–2581.

Peñuelas J, Sardans J, Ogaya R, Estiarte M (2008a) Nutrient stoichiometric relations and biogeochemical niche in coexisting plant species: effect of simulated climate change. *Polish Journal of Ecology*, **56**, 613–622.

Peñuelas J, Hunt JM, Ogaya R, Jump AS (2008b) Twenthieth century changes treering 13C at the southern range-edge of *Fagus sylvatica*: increasing water-use efficiency does not avoid the growth decline induced by warming at low altitudes. *Global Change Biology*, **14**, 1076–1088.

Peñuelas J, Rutishauser T, Filella I (2009a) Phenology Feedbacks on Climate Change. *Science*, **324**, 887–888.

Peñuelas J, Lilella I, Seco R, Llusia J (2009b) Increase isoprene and monoterpene emissions after re-watering of droughted *Quercus ilex* seedlings. *Biologia Plantarum*, **53**, 351–354.

Peñuelas J, Carnice J. (2010) Climate change and peak oil: the urgent need for a transition to a non-carbon-emitting society. AMBIO: A Journal of the Human Environment, **39**(1) 85–90.

Peñuelas J, Canadell JG, Ogaya R (2011a) Increased water-use efficiency during the 20th century did not translate into enhanced tree growth. *Global Ecology and Biogeography*, **20**, 597–608.

Peñuelas J, Garbulsky M, Filella I (2011b) Photochemical reflectance index (PRI) and remote sensing of plant CO_2 uptake. *New Phytologist*, **191**, 596–599.

Peñuelas J, Sardans J, Rivas-Ubach A, Janssess I (2012) The human-induced imbalances between C, N and P in Earth's life system. *Global Change Biology*, **18**, 3–6.

Perera IY, Hung CY, Moore GD, Stevenson-Paulik J, Boss WF (2008) Transgenic *Arabidopsis* plants expressing the type 1 inositol 5-phosphatase exhibit increased drought tolerance and altered abcisic acid signaling. *The Plant Cell*, **20**, 2876–2893.

Perez DE, Hoyer JS, Johnson AI, Moody ZR, Lopez J, Kaplinsky NJ (2009) BOBBER1 is a noncanonical *Arabidopsis* small heat shock protein requires for both development and thermotolerance. *Plant Physiology*, **151**, 241–252.

Pérez-Ramos IM, Ourcival JM, Limousin JM, Rambal, (2010) Maet seeding under increasing drought: results from a long-term data set and from a rainfall exclusion experiment. *Ecology*, **91**, 3057–3068.

Petchey OL, McPhearson PT, Casey TM, Morin PJ (1999) Environment warming alters food-web structure and ecosystem function. *Nature*, **402**, 69–72.

Peters GP, Marland G, Le Quéré C, Boden T, Canadell JG, Raupach MR (2012) Rapid growth in CO2 emissions after the 2008–2009 global financial crisis. *Nature Climate Change*, **2**, 2–4.

Petit JR, Jouzel J, Raunaud D *et al*. (1999) Climate and atmospheric history of the past 420,000 years from the Vostok ice core, Antarctica. *Nature*, **339**, 429–436.

Peuke AD, Rennenberg H (2004) Carbon, nitrogen, phosphorus, and sulphur concentration and partitioning in beech ecotypes (*Fagus sylvatica* L): phosphorus most affected by drought. *Trees*, **18**, 639–648.

Pigott CD, Pigott S (1993) Water as a determinant of the distribution of trees at the boundary of the Mediterranean zone. *Journal of Ecology*, **81**, 557–566.

Pinheiro C, Passarinho JA, Ricardo CP (2004) Effect of drought and rewatering on the metabolism of *Lupinus albus* organs. *Journal of Plant Physiology*, **161**, 1203–1210.

Plomion C, Lalanne C, Claverol S *et al*. (2006) Mapping the proteome of poplar and application to the discovery of drought-stress responsive proteins. *Proteomics*, **6**, 6509–6527.

Pluskal T, Nakamura T, Villar-Briones A, Yanagida M (2010) Metabolic profiling of the fission yeast *S. pombe*: quantification of compounds under different temperatures and genetic perturbation. *Molecular Biosystems*, **6**, 182–198.

Post E, Peterson RO, Stenseth NC, McLaren BE (1999) Ecosystems consequences of wolf behavioural response to climate. *Nature*, **401**, 905–907.

Post E, Pedersen C, Wilmers CC, Forchhammer MC (2008) Warming, plant phenology and the spatial dimension of trophic mismatch for large herbivores. *Proceedings of the Royal Society B*, **275**, 2005–2013.

Potti J (2009) Advance breeding dates in relation to recent climate warming in a Mediterranean montane population of Blue tits *Cyanites caeruleus*. *Journal of Ornithology*, **150**, 893–901.

Pretzsch H, Dieler J (2011) The dependency of the size-growth relastionship of Norway spruce (*Picea abies* [L.] Karst.) and European beech (*Fagus sylvatica* [L.]) in forest stands on long-term site conditions, drought events, and ozone stress. *Trees*, **25**, 355–369.

Price MV, Waser NM (1998) Effects of experimental warming on plant productive phenology in a subalpine meadow. *Ecology*, **79**, 1261–1271.

Price MV, Waser NM (2000) Responses of subalpine meadow vegetation to four years of experimental warming. *Ecological Applications*, **10**, 811–823.

Prieto P, Peñuelas J, Ogaya R, Estiarte M (2008) Precipitation-dependent flowering of *Globularia alypum* and *Erica multiflora* in Mediterranean shrubland under experimental drought and warming, and its inter-annual variability. *Annals of Botany*, **102**, 275–285.

Prieto P, Peñuelas P, Llusia J, Asensio D, Estiarte M (2009a) Effects of long-term experimental night-time warming and drought on photosynthesis, Fv/Fm and stomatal conductance in the dominant species of a Mediterranean shrubland. *Acta Physiologica Plantarum*, **31**, 729–739.

Prieto P, Peñuelas J, Llusia J, Asensio D, Estiarte M (2009b) Effects of experimental warming and drought on biomass accumulation in a Mediterranean shrubland. *Plant Ecology*, **205**, 179–191.

Prieto P, Peñuelas J, Niinemetts Ü *et al*. (2009c) Changes in the onset of spring growth in shrubland species in response to experimental warming along a north-south gradient in Europe. *Global Ecology and Biogeography*, **18**, 473–484.

Prieto P, Peñuelas J, Lloret F, Llorens L, Estiarte L (2009d) Experimental drought and warming decrease diversity and slow down post-fire succession in a Mediterranean. *Ecography*, **32**, 623–636.

Pritchard J, Griffiths B, Hunt J (2007) Can the plant-mediated impacts on aphids of elevated CO2 and drought be predicted? *Global Change Biology*, **13**, 1616–1629.

Priyanka B, Sekhar K, Reddy VD, Rao KV (2010) Expression of pigeonpea hybrid-proline-rich protein encoding gene (CcHyPRP) in yeast and Arabidopsis affords multiple abiotic stress tolerance. *Plant Biotechnology Journal*, **8**, 76–87.

Pulido F, Berthold P (2004) Microevolutionary response to climate change. *Advances in Ecological Research*, **35**, 151–183.

Qaderi MM, Kurepin LV, Reid DM (2006) Growth and physiological responses of canola (Brassica napus) to three components of global climate change: temperature, carbon dioxide and drought. *Physiology Plantarum*, **128**, 710–721.

Qin F, Sakuma Y, Tran LSP *et al*. (2008) Arabidopsis DREB2A-interacting proteins function as RINGE3 ligases and negatively regulate plant drought stress-responsive gene expression. *The Plant Cell*, **20**, 1693–1707.

Rabello A, Guimaraes CM, Rangel PHN *et al*. (2008) Identification of drought-responsive genes in roots of upland rice (*Oryza sativa* L). *BMC Genomics*, **9**, 485.

Ramírez V, Coego A, López A, Agorio A, Flors V, Vera P (2009) Drought tolerance in Arabidopsis is controlled by the OCP3 disease resistance regulator. *The Plant Cell*, **58**, 578–581.

Rampino P, Pataleo S, Gerardi C, Mita G, Perrotta C (2008) Drought stress response in wheat: physiological and molecular analysis of resistant and sensitive genotypes. *Plant Cell and Environment*, **29**, 2143–2152.

Reed SC, Coe KK, Sparks JP, Housman DC, Zelikova TJ, Belnap J (2012) Chages to dryland rainfall result in rapid moss mortality and altered soil fertility. *Nature Climate Change*, doi:10.1038/NCLIMATE1596.

Regier N, Streb S, Cocozza C, Schaub M, Cherubini P, Zeeman SC, Frey B (2009) Drought tolerance of two black poplar (*Populus nigra* L.) clones: contribution of carbohydrates and oxidative stress defence. *Plant Cell and Environment*, **32**, 1724–1736.

Rennenberg H, Loreto F, Polle A, Brilli F, Fares S, Beniwal RS, Gessler A (2006) Physiological responses of forest trees to heat and drought. *Plant Biology*, **8**, 556–571.

Renzhong W, Qiong G. (2003) Climate-driven changes in shoot density and shoot biomass in Leymus chinensis (Poaceae) on the North-east China transect (NECT). *Global Ecology & Biogeography*, **12**, 249–259.

Reynolds JF, Virginia RA, Kemp PR, De Soyza AG, Tremmel DC (1999) Impact of drought on desert shrubs: effects of seasonality and degree of resource island development. *Ecological Monographs*, **69**, 69–106.

Rillig MC, Wright SF, Shaw MR, Field CB (2002) Artificial climate warming positively affects asbuscular mycorrhizas but decreases soil aggregates water atability in an annual grassland. *Oikos*, **97**, 52–58.

Ripley B, Frole K, Gilbert M (2010) Differences in drought sensitivities and photosynthetic limitations between co-occuring C3 and C4 (NADP-ME) panicoid grasses. *Annals of Botany*, **105**, 493–503.

Rivas-Ubach A, Sardans J, Pérez-Trujillo M, Estiarte M, Peñuelas J (2012) Strong relationship between elemental stoichiometry and metabolome in plants. *Proceedings of the National Academy of Sciences of the United States of America*, **109**, 4181–4186.

Rivero RM, Shulaev V, Blumwald E (2009) Cytokinin-dependent photorespiration and the protection of photosynthesis during water deficit. *Plant Physiology*, **150**, 1530–1540.

Rizhsky L, Liang HJ, Shuman J, Shulaev V, Davletova S, Mittler R (2004) When defense pathways collide. The response of *Arabidopsis* to a combination of drought and heat stress. *Plant Physiology*, **134**, 1683–1696.

Rollinson CR, Kaye MW (2012) Experimental warming alters spring phenology of certain plant functional groups in an early successional forest community. *Global Change Biology*, **18**, 1108–1116.

Roy BA, Güsewell S, Harte J (2004) Response of plant pathogens and herbivores to a waerming experiment. *Ecology*, **85**, 2570–2581.

Rull V, Vegas-Vilarrubia TA (2006) Unexpected biodiversity loss under global warming in the neotropical Guayana highlands: a preliminary appraisal. *Global Change Biology*, **12**, 1–9.

Rustad LE, Campbell JL, Marion GM *et al.* (2001) A meta-analysis of the response of soil respiration, net nitrogen mineralization, and aboveground plant growth to experimental ecosystem warming. *Oecologia*, **126**, 543–562.

Sakuma Y, Maruyama K, Osakabe Y, Qin F, Seki M, Shinozaki K, Yamaguchi-Shinozaki K (2006) Functional analysis of an Arabidopsis transcription factor. DREB2A, involved in drought-responsive gene expression. *The Plant Cell*, **18**, 1292–1309.

Salvaudon L, Giraud T, Shykoff JA (2008) Genetic diversity in natural populations: a fundamental component of plant-microbe interactions. *Current Opinion in Plant Biology*, **11**, 135–143.

Sanchez DH, Schwabe F, Erban A, Udvardi MK, Kopka J (2012) Comparative metabolomics of drought acclimation in model and forage legumes. *Plant Cell and Environment*, **35** (136), 149.

Sardans J, Peñuelas P (2004) Increasing drought decreases phosphorus availability in an evergreen Mediterranean forest. *Plant and Soil*, **267**, 367–377.

Sardans J, Peñuelas J (2005) Drought decreases soil enzyme activity in a Mediterranean holm oak forest. *Soil Biology and Biochemistry*, **37**, 455–461.

Sardans J, Peñuelas J (2007) Drought changes phosphorus and potassium accumulation patterns in an evergreen Mediterranean forest. *Functional Ecology*, **21**, 191–201.

Sardans J, Peñuelas J (2010) Soil enzyme activity in a Mediterranean forest after six years of drought. *Soil Science Society of American Journal*, **74**, 838–851.

Sardans J, Peñuelas J, Estiarte M (2007) Seasonal patterns of root-surface phosphatase activities in a Mediterranean shrubland. Responses to experimnetal warming and drought. *Biology and Fertility of Soils*, **43**, 779–786.

Sardans J, Peñuelas J, Estiarte M, Prieto P (2008a) Warming and drought alter C and N concentration, allocation and accumulation in a Mediterranean shrubland. *Global Change Biology*, **14**, 2304–2316.

Sardans J, Peñuelas M, Estiarte M (2008b) Changes in soil enzymes related to C and N cycle and in soil C and N content under prolonged warming and drought in a Mediterranean shrubland. *Applied Soil Ecology*, **39**, 223–235.

Sardans J, Peñuelas J, Ogaya R (2008c) Experimental drought reduced acid and alkaline phosphatases activity and increase organic extractable P in soil in a *Quercus ilex* Mediterranean forest. *European Journal of Soil Biology*, **44**, 509–520.

Sardans J, Peñuelas J, Lope-Piedrafita S (2010) Changes in water content and distribution in *Quercus ilex* during progressive drought assessed by in vivo ^{1}H magnetic resonance imaging. *BMC Plant Biology*, **10**, 188.

Sardans J, Peñuelas J, Rivas-Ubach A (2011) Ecological metabolomics: overview of current developments and future challenges. *Chemoecology*, **21**, 191–225.

Sardans J, Rivas-Ubach A, Peñuelas J (2012a) The elemental stoichiometry of aquatic and terrestrial ecosystems and its relationships with organismic lifestyle and ecosystem structure and function: a review and perspectives. *Biogeochemistry*, **111**, 1–39.

Sardans J, Rivas-Ubach A, Peñuelas J (2012b) The C:N:P stoichiometry of organisms and ecosystems in a changing world: a review and perspectives. *Perspectives in Plant Ecology Evolution and Systematics*, **14**, 33–47.

Sarkar NK, Kim YK, Grover A (2009) Rice sHsp genes: genomic organization and expression profiling under stress and development. *BMC Genomics*, **10**, 393.

Saxe H, Cannell MGR, Sen OJ, Ryan MG, Vourlitis G (2001) Tree and forest functioning in response to global warming. *New Phytologist*, **149**, 369–400.

Saxena RK, Cui X, Thakur V, Walter B, Close TJ, Varshney RK (2011) Single feature polymosphisms (SFPs) for drought tolerance in pigeonpea. *Functional Integrative Genomics*, **11**, 651–657.

Schaefer T, Ledebur G, Beier J, Leisler B (2006) Reproductive responses of two related coexisting songbird species to environmental changes: global warming. Competition and population size. *Journal of Ornithology*, **147**, 47–56.

Scherrer D, Körner C (2011) Topographically controlled thermal-habitat differentiation buffers alpine plant diversity against climate warming. *Journal of Biogeography*, **38**, 406–416.

Schmidt IK, Jonasson S, Shaver GR, Michelsen A, Nordin A (2002) Mineralization and distribution of nutrients in plants and microbes in four Arctic ecosystems: response to warming. *Plant and Soil*, **242**, 93–106.

Schramm F, Larkindale J, Kiehlman E, Ganguli A, Englich G, Vierling E, von Koskull-Döring P (2008) A cascade of transcription factor DREB2A and heat stress transcription factor HsfA3 regulates the heat stress response of *Arabidopsis*. *The Plant Journal*, **53**, 264–274.

Schulte GG, Elnitsky MA, Benoit JB, Denliger DL, Lee RE Jr (2008) Extremely large aggregations of collembolan eggs on Humble Island, Antartica: a response to early warming? *Polar Biology*, **31**, 889–892.

Schwartz MD (1996) Examining the spring discontinuity in daily temperature ranges. *Journal of Climate*, **9**, 803–808.

Schwinning S, Starr BI, Ehleringer JR (2005) Summer and winter drought in a cold desert ecosystem (Colorado Plateau) part II: effects on plant carbon assimilation and growth. *Journal of Arid Environments*, **61**, 61–78.

Scriber JM (2011) Impacts of climate warming of hybrid zone movement: geographically diffuse and biologically porous “species borders”. *Insect Science*, **18**, 121–159.

Scriber JM, Ording GJ (2005) Ecological speciation without host plant specialization; possible origins of a recently described cryptic Papilio species. *Entomologia Experimentalis et Applicata*, **115**, 247–263.

Sergeant K, Spieb N, Renaut J, Wilhelm E, Hausman JF (2011) One dry summer: a leaf proteome study on the response of oak to drought exposure. *Journal of Proteomics*, **74**, 1385–1395.

Selas V, Sonerud GA, Framstad E, Kalas JA, Kobro S, Pedersen Spidso TK, Wiig O (2011) Climate change in Norway; warm summers limit grouse reproduction. *Population Ecology*, **53**, 361–371.

Seiler C, Harshavardhan VT, Rajesh K *et al.* (2011) ABA biosynthesis and degradation contributing to ABA homeostasis during barley seed development under control and terminal drought-stress conditions. *Journal of Experimental Botany*, **62**, 2615–2632.

Semel Y, Schauer N, Roessner U, Zamir D, Fernie AR (2007) Metabolite analysis for the comparison of irrigated and non-irrigated field grown tomato of varying genotype. *Metabolomics*, **3**, 289–295.

Seo PJ, Xiang F, Qiao M *et al.* (2009) The MYB96 transcription factor mediates abscisic acid signaling during drought stress response in *Arabidopsis*. *Plant Physiology*, **151**, 275–289.

Serrano L, Peñuelas P (2005) Contribution of physiological and morphological adjustments to drought resistance in two Mediterranean tree species. *Biologia Plantarum*, **49**, 551–559.

Shao HB, Chu LY, Jaleel CA, Zhao CX (2008) Water-deficit stress-influenced anatomical changes in higher plants. *C R Biologies*, **331**, 215–225.

Shaver GR, Jonasson S (1999) Response of arctic ecosystem to climate change: results of long-term field experiments in Sweden and Alaska. *Polar Research*, **18**, 245–252.

Shaver GR, Canadell J, Chapin FS III *et al.* (2000) Global warming and terrestrial ecosystems: a conceptual framework for analysis. *BioScience*, **50**, 871–882.

Shaw MR, Zavaleta ES, Chiariello NR, Cleland EE, Mooney H, Field CB (2002) Grassland responses to global environmental changes suppressed by elevated CO2. *Science*, **298**, 1987–1990.

Sherry RA, Zhou X, Gu S *et al.* (2007) Divergence of reproductive phenology under climate warming. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 198–202.

Shi L, Guttenberger M, Kottke I, Hampp R (2002) The effect of drought on mycorrhizas of beech (Fagus sylvatica L.): changes in community structure, and the content of carbohydrates and nitrogen storage bodies of the fungi. *Mycorrhiza*, **12**, 303–311.

Shi FS, Wu Y, Wu N, Luo P (2010) Different growth and physiological responses to experimentañ warming of two dominant plant species *Elymus nutants* and *Potentilla anserine* in an alpine meadow of the eastern Tibetan Plateau. *Photosynthetica*, **48**, 437–445.

Shoo LP, Williams SE, Hero JM (2005) Climate warming and the rainforest birds of the Australian wet tropics: using abundance data as a sensitive predictor of change in total population size. *Biological Conservation*, **125**, 335–343.

Signarbieux C, Feller U (2011) Non-stomatal limitations of photosynthesis in grassland species under artificial drought in the field. *Environmental and Experimental Botany*, **71**, 192–197.

Sjursen H, Michelsen A, Jonasson S (2005) Effects of long-term soil warming and fertilization on microarthropod abundances in three sub-artic ecosystems. *Applied Soil Ecology*, **30**, 148–161.

Song L, Chow WS, Sun L, Li C, Peng C (2010) Acclimation of photosystem II to high temperature in two Wedelia species from different geographical origins: implications for biological invasions upon global warming. *Journal of Experimental Botany*, **61**, 4087–4096.

Sorensen PL, Michelsen A (2011) Long-term warming and litter additions affects nitrogen fixation in a subartic heath. *Global Change Biology*, **17**, 528–537.

Spieb N, Oufir M, Matusikova I *et al.* (2012) Ecophysiological and transcriptomic responses of oak (*Quercus robur*) to long-term drought exposure and rewatering. *Environmental and Experimental Botany*, **77**, 117–126.

Staddon PL, Gregersen R, Jakobsen I (2004) The response of two *Glomus* mycorrhizal fungi and a fine endophyte to elevated atmospheric CO$_2$, soil warming and drought. *Global Change Biology*, **10**, 1909–1921.

Starr G, Oberbauer SF, Ahlquist LE (2008) The phoptosynthetic response of Alaskian tundra plants to increased season length and soil warming. *Arctic Antartic and Alpine Research*, **40**, 181–191.

Stefanescu C, Peñuelas J, Filella I (2003) Effect of climatic change on the phenology of butterflies in the northwest Mediterranean Basin. *Global Change Biology*, **9**, 1491–1506.

Stefanescu C, Carnicer J, Peñuelas J (2011) Determinants of species richness in generalist and specialist Mediterranean butterflies: the negative synergic forces of climate and habitat change. *Ecography*, **34**, 353–363.

Steltzer H, Post E (2009) Seasons and life cycles. *Science*, **324**, 886–887.

Stenstrom M, Gugerli F, Henry GHR (1997) Response of *Saxifraga opositifolia* L. to simulated climate change a three contrasting latitudes. *Global Change Biology*, **3** (Suppl. 1), 44–54.

Stirling CM, Heddell-Cowie M, Jones ML, Ashenden TW, Sparks TH (1998) Effects of elevated CO2 and temperature on growth and allometry of five native fast-growing annual species. *New Phytologist*, **140**, 343–353.

Storz JF (2005) Using genome scans of DNA polymorphism to infer adaptive population divergence. *Molecular Ecology*, **14**, 671–688.

Street NR, Skogström O, Sjödin A *et al.* (2006) The genetics and genomics of the drought response in *Populus*. *The Plant Journal*, **48**, 321–341.

Sumerford DV, Abrahamson WG, Weis AE (2000) The effects of drought on the Solidago altissima-Eurosta solidaginis-natural enemy complex: population dynamics, local extirpations, and measures of selection intensity on gall size. *Oecologia*, **122**, 240–248.

Swarbreck SM, Sudderth EA, St. Clair SB, Salve R, Castanha C, Torn MS, Ackerly DD, Andersen GL, (2011) Linking leaf transcript levels to whole plant analyses provides mechanistic insights to the impact of warming and altered water availability in an annual grass. *Global Change Biology*, **17**, 1577–1594.

Takeda K, Musolin DL, Fujtsaki K (2010) Dissecting insect responses to climate warming: overwintering and post-diapause performance in the southern green stink bug, *Nezara viridula*, under simulated climate-change conditions. *Physiological Entomology*, **35**, 343–353.

Tans P (2012) NOAA/ESRL and Dr. Ralph Keeling, Scripps Institution of Oceanography (scrippsco2.ucsd.edu/). Available at: www.esrl.noaa.gov/gmd/ccgg/trends/ (accessed 18 September 2012)

Thiel D, Nagy L, Beierkuhnlein C, Huber G, Jentsch A, Konnert M, Kreyling J (2012) Uniform drought and warming responses in Pinus nigra provenances despite specific overall performances. *Forest Ecology and Management*, **270**, 200–208.

Thórhallsdóttir TE (1998) Flowering phenology in the central highland of Iceland and implications for climatic warming in the Arctic. *Oecologia*, **114**, 41–49.

Tilman D, Haddi A (1992) Drought and biodiversity in grasslands. *Oecologia*, **89**, 257–264.

Tobin PC, Nagarkatt S, Loeb G, Saunders MC (2008) Historial and projected interactions between climate change and insect voltinism in a multivoltine species. *Global Change Biology*, **14**, 951–957.

Tucker JK, Dolan CR, Lamer JT, Dustman EA (2008) Climatic warming, sex ratios, and red-eared sliders (*Trachemys scripta elegans*) in Illinois. *Chelonian Conservation and Biology*, **7**, 60–69.

Turner MA, Viant MR, Teh SJ, Johnson ML (2007) Developmental rates, structural asymmetry, and metabolic fingerprints of steelhead trout (*Oncorhynchus mykiss*) eggs incubated at two temperatures. *Fish Physiology and Biochemistry*, **33**, 59–72.

Urano K, Maruyama K, Ogata Y *et al.* (2009) Characterization of the ABA-regulated global responses to dehydration in Arabidopsis by metabolomics. *The Plant Journal*, **57**, 1065–1078.

Van Bogaert R, Jonasson C, De Dapper M, Callaghan TV (2009) Competitive interaction between aspen and birch moderated by invertebrate and vertebrate herbivores and climate warming. *Plant Ecology and Diversity*, **2**, 221–232.

Verlinden M, Nijs I (2010) Alien plants species favoured over congeneric natives under experimental climate warming in temperate Belgian climate. *Biological Invasions*, **12**, 2777–2787.

Viant MR, Werner I, Rosenblum ES, Gantner AS, Tjeerdema RS, Johnson ML (2003) Correlation between heat-shock protein induction and reduced metabolic condition in juvenile steelhead trout (*Oncorhynchus mykis*s) chronically exposed to elevated temperature. *Fish Physiology and Biochemistry*, **29**, 159–171.

Volder A, Edwards EJ, Evans JR, Robertson BC, Schortemeyer M, Gifford RM (2004) Does greater night-time, rather than constant, warming alter growth of managed pasture under ambient and elevated atmospheric CO$_2$? *New Phytologist*, **162**, 397–411.

Volder A, Tjoelker MG, Briske DD (2010) Contrasting physiological responsiveness of establishing trees and a C4 grass to rainfall events, intensified summer drought, and warming in oak savanna. *Global Change Biology*, **16**, 3349–3362.

Waagner D, Heckmann LH, Malmendal A, Nielsen NC, Holmstrup M, Bayley M (2010) Hsp70 expression and metabolite composition in response to short-term thermal changes in *Folsomia candida* (Collembola). *Comparative Biochemistry and Physiology – Part A: Molecular and Integrative Physiology*, **157**, 177–183.

Wada N, Shimono M, Miyamotto M, Kojima S (2002) Warming effects on shoot development growth and biomass production in sympatric evergreen alpine dwarf shrubs *Empetrum nigrum* and *Loiseleuria procumbens*. *Ecological Research*, **17**, 125–132.

Wahren CHA, Walker MD, Bret-Harte MS (2005) Vegetation responses in Alaskan artic tundra after 8 years of a summer warming and winter snow manipulation experiment. *Global Change Biology*, **11**, 537–552.

Walker MD, Wahren CH, Hollister RD *et al.* (2006) Plant community responses to experimental warming across the tundra biome. *Proceedings of the National Academy of Sciences of the United States of America*, **103**, 1342–1346.

Walther GR (2003) Plants in a warmer world. *Perspectives in Plant Ecology Evolution and Systematics*, **6**, 169–185.

Wan S, Norby RJ, Pregitzer KS, Ledford J, O'Neill EG (2004) CO2 enrichment and warming of the atmosphere enhance both productivity and mortality of maple tree fine roots. *New Phytologist*, **162**, 437–446.

Wan SQ, Hui DF, Wallace L, Luo YQ (2005) Direct and indirect effects of experimental warming on ecosystem carbon processes in a tallgrass praire. *Global Biogeochemical Cycles*, **19**, GB2014.

Wan S, Xia J, Liu W, Niu S (2009) Photosynthetic overcompensation under nocturnal warming enhances grassland carbon sequestration. *Ecology*, **90**, 2700–2710.

Wang JP, Bughrara SS (2007) Monitoring of gene expression profiles and identification of candidate genes involved in drought responses in *Festuca mairei*. *Molecular Genetic Genomics*, **277**, 571–587.

Wang Y, Beaith M, Chalifoux M *et al.* (2009) Shoot-specific down-regulation of protein farnesyltransferase (a-subunit) for yield protection against drought in Canola. *Molecular Plant*, **2**, 191–200.

Wang W, Liu X, An W, Xu G, Zeng X (2012) Increased intrinsic water-use efficiency during a period with persistent decreased tree radial growth in northwestern China: causes and implications. *Forest Ecology and Management*, **275**, 14–22.

Watkinson JI, Hendricks L, Sioson AA, Heath LS, Bohnert HJ, Grene R (2008) Tuber development phenotypes in adapted and acclimated drought-stressed *Solanum tuberosum* ssp. *andigena* have distinct expression profiles of genes associated with carbon metabolism. *Plant Physiology and Biochemistry*, **46**, 34–45.

Warren CR, Aranda I, Cano FJ (2012) Metabolomic demonstrates divergent responses of two Eucalyptus species to water stress. *Metabolomics*, **8**, 186–200.

Weltzin JF, Pastor J, Harth C, Bridgham SD, Updegraff K, Chapin CT (2000) Response of bog and fen plant communities to warming and water-table manipulations. *Ecology*, **81**, 3464–3478.

Weltzin JF, Bridgham SD, Pastor J, Chen J, Harth C (2003) Potential effects of warming and drying on peatland plant community composition. *Global Change Biology*, **9**, 141–151.

Wertin TM, McGuire MA, Teskey RO (2012) Effects of predicted future and current atmospheric temperature and [CO_2] and high and low soil moisture on gas exchange and growth of *Pinus taeda* seedlings at cool and warm sites in the species range. *Tree Physiology*, **32**, 847–858.

Wessel WW, Tietema A, Beier C, Emmett BA, Peñuelas J, Riis-Nielsen T (2004) A qualitative ecosystem assessment for different shrublands in western Europe under impact of climate change. *Ecosystems*, **7**, 662–671.

West AG, Dawson TE, February EC, Midgley GF, Bond WJ, Aston TL (2012) Diverse functional responses to drought in Mediterranean-type shrubland in South Africa. *New Phytologist*, **195**, 396–407.

Williams DG, Black RA (1994) Drought response of a native and introduced Haeaiian grass. *Oecologia*, **4**, 512–518.

Williams AL, Wills KE, Janes JK, Vander Schoor JK, Newton PCD, Hovenden MJ (2007) Warming and free-air CO_2 enrichment alter demographics in four co-occurring grassland species. *New Phytologist*, **176**, 365–374.

Wilson PB, Estavillo GM, Field KJ *et al.* (2009) The nucleotidase/phosphatise SAL1 is a negative regulator of drought tolerance in Arabidopsis. *The Plant Journal*, **58**, 299–317.

Wolkovich EM, Cook BI, Allen JM *et al.* (2012) Warming experiments underpredict plant phonological responses to climate change. *Nature*, **485**, 494–497.

Worrall JJ, Egeland L, Eager T, Mask RA, Johnson EW, Kemp PA, Shepperd WD (2008) Rapid mortality of *Populus tremuloides* in southern Colorado, USA. *Forest Ecology and Management*, **225**, 686–696.

Wu Z, Koch GW, Dijkstra P, Bowker MA, Hungate BA (2011a) Responses of ecosystem carbon cycling to climate change treatments along an elevation gradient. *Ecosystems*, **14**, 1066–1080.

Wu Z, Dijkstra P, Koch GW, Peñuelas J, Hungate BA (2011b) Responses of terrestrial ecosystems to temperature and precipitation change: a meta-analysis of experimental manipulation. *Global Change Biology*, **17**, 927–942.

Wu Z, Dijkstra P, Koch GW, Hungate BA (2012) Biogeochemical and ecological feedbacks in grassland responses to warming. *Nature Climate Change*, **2**, 458–461.

Xia J, Niu S, Wan S (2009) Response of ecosystem carbon exchange to warming and nitrogen addition during two hydrologically contrasting growing seasons in a temperate steppe. *Global Change Biology*, **15**, 1544–1556.

Xiao X, Yang F, Zhang S, Korpelainen H, Li C (2009) Physiological and proteomic responses to two contrasting *Populus cathayana* populations to drought stress. *Physiologia Plantarum*, **136**, 150–168.

Xu Y, Huang B (2008a) Differential protein expression for geothermal *Agrostis scabra* and turf-type *Agrostis stolonifera* differing in heat tolerance. *Environmental and Experimental Botany*, **64**, 58–64.

Xu C, Huang B (2008b) Root proteomic responses to heat stress in two *Agrostis* grass species contrasting in heat tolerance. *Journal of Experimental Botany*, **59**, 4183–4194.

Xu C, Huang B (2010) Differential proteomic response to heat stress in thermal *Agrostis scabra* and heat-sensitive *Agrostis stolonifera*. *Physiologia Plantarum*, **139**, 194–204.

Xu ZZ, Zhou GS (2006) Nitrogen metabolism and photosynthesis in *Leymus chinensis* in response to long-term soil drought. *Journal of Plant Growth Regulation*, **25**, 252–266.

Xu Z, Zhou G, Wang Y (2007) Combined effects of CO2 and soil drought on carbon and nitrogen allocation of the desert shrub Caragana intermedia. *Plant and Soil*, **301**, 87–97.

Xu J, Belanger F, Huang B (2008) Differential gene expression in shoots and roots under heat stress for a geothermal and non-thermal *Agrostis grass* species contrasting in heat tolerance. *Environmental and Experimental Botany*, **63**, 240–247.

Xu ZF, Hu TX, Wang KY, Zhang YB, Xian JR (2009) Short-term responses of phenology, shoot growth and leaf traits of four alpine shrubs in a timberline ecotone to simulated global warming, eastern Tibetan Plateau, China. *Plant Species Biology*, **24**, 27–34.

Yaire J, van Cleve K (1996) Effects of carbon, fertilizer and drought on foliar chermistry of tree species in interior Alaska. *Ecological Applications*, **6**, 815–827.

Yamakawa H, Hakata M (2010) Atlas of rice grain filling-related metabolism under high temperature: joint analysis of metabolome and transcriptome demonstrated inhibition of starch accumulation and induction of amino acid accumulation. *Plant and Cell Physiology*, **51**, 795–809.

Yang F, Wang Y, Miao LF (2010) Comparative physiological and proteomic responses to drought stress in two poplar species originating from different altitudes. *Physiologia Plantarum*, **139**, 399–400.

Yang F, Jorgensen AD, Li H *et al.* (2011) Implications of high-temperature events and water deficits on protein profiles in wheat (*Triticum aestivum* L. cv. Vinjett) grain. *Proteomics*, **11**, 1884–1895.

Yavitt JB, Wright SJ, Weider RK (2004) Seasonal drought and dry-season irrigation influence leaf-litter nutrients and soil enzymes in a moist, lowland forest in Panama. *Austral Ecology*, **29**, 177–188.

Yergeau E, Bokhorst S, Kang S, Zhou J, Greer CW, Aerts R, Kowalchuk GA (2012) Shifts in soil microorganism in response to warming are consistent across a range of Antartic environments. *ISME Journal*, **6**, 692–702.

Yin HJ, Liu Q, Lai T (2008) Warming effects on growth and physiology in the seedlings on the two conifers Picea asperata and Abies faxoniana under two contrasting light conditions. *Ecological Research*, **23**, 459–469.

Yurkonis KA, Meiners Sj (2006) Drought impacts and recovery are driven by local variation in species turn-over. *Plant Ecology*, **184**, 325–336.

Yuste JC, Peñuelas J, Estiarte M *et al.* (2011) Drought-resistant fungi control soil organic matter decomposition and its response to temperature. *Global Change Biology*, **17**, 1475–1486.

Zaitchik BF, Macalady AK, Bonneau LR, Smith RB (2006) Europe's 2003 heat wave: a satellite view of impacts and land-atmosphere feedbacks. *International Journal of Climatology*, **26**, 743–769.

Zelikova TJ, Housman DC, Grote EE, Neher DA, Belnap J (2012) Warming and increased precipitation frequency of the Colorado plateau: implications for biological soil crusts and soil processes. *Plant and Soil*, **355**, 262–282.

Zhang Y, Mian MAR, Chekhovsky K, So S, Kupter D, Lai H, Roe BA (2005a) Differential gene expression in Festuca under heat stress conditions. *Journal of experimental Botany*, **56**, 897–907.

Zhang W, Parker KM, Luo Y, Wan S, Wallace LL, Hu S (2005b) Soil microbial responses to experimental warming and clipping in a tallgrais prairie. *Global Change Biology*, **11**, 266–277.

Zhang H, Ohyama K, Boudet J *et al.* (2008) Dolichol biosynthesis and its effects on the unfolded protein response and abiotic stress resistance in Arabidopsis. *The Plant Cell*, **20**, 1879–1898.

Zhang F, Li Y, Guo Z, Murray BR (2009) Climate warming and reproduction in Chinese alligators. *Animal Conservation*, **12**, 128–137.

Zhang S, Chen F, Peng S, Ma W, Korpelainen H, Li C (2010a) Comparative physiological, ultrastructural and proteomic analyses reveal sexual differences in the responses of *Populus cathayana* under drought stress. *Proteomics*, **10**, 2661–2677.

Zhang M, Li G, Huang W *et al.* (2010b) Proteomic study of Carissa spinarum in response to combined heat and drought stress. *Proteomics*, **10**, 3117–3129.

Zhang J, John UP, Wang Y *et al.* (2011a) Targeted mining of drought stress-responsive genes from EST resources in Cleistrogenes songorica. *Journal of Plant Physiology*, **168**, 1844–1851.

Zhang R, Jongejans E, Shea K (2011b) Warming increases the spread of an invasive Thistle. *PLoS ONE*, **6**, e21725.

Zhao MS, Running SW (2010) Drought-induced reduction in global terrestrial net primary production from 2000 through 2009. *Science*, **329**, 940–943.

Zhou X, Liu X, Wallace LL, Luo Y (2007) Photosynthetic and respiratory acclimation to experimental warming for four species in a tallgrass prairie ecosystem. *Journal of Integrative Plant Biology*, **49**, 270–281.

Zhu Y, Wang Z, Jing Y, Wang L, Liu X, Liu Y, Deng X (2009) Ectopic over-expression of BhHsf1, a heat shock factor from the resurrection plant Boea hygrometrica, leads to increased thermotolerance and retarded growth in transgenic *Arabidopsis* and tobacco. *Plant Molecular Biology*, **71**, 451–467.