Table 1 **Trends in annual snow accumulation at the Mount Logan ice core site**

Time interval	1736–1850	1851–2000	1948–2000	1976–2000
Trend (m per decade)	0.003	0.008	0.034	0.12
Significance level (%)	50	95	95	99

period of overlap between it and the Mount Logan time series, 1736–1991, there is no statistically significant correlation between them.

The complex relationship between the Mount Logan time series, the PNA and the PDO identified in this paper is not unique. For example, the correlation between salmon productivity in Alaska and the PDO[24], although robust over the past 50 years, shows changes in correlation and phase when 300-year proxy reconstructions of North Pacific sea surface temperature and salmon abundance are compared[25]. This complexity serves to highlight the need to constrain better the temporal and spatial variability of climatic modes, such as the PDO and PNA, using several independent proxies in order to better predict their evolution and their relevance to societal concerns[2,26].

The three-century-long snow-accumulation record from the Mount Logan site extends from the closing stages of the Little Ice Age to the warmest decade in the past millennium[7]. A statistically significant and accelerating positive trend has existed in this time series since the middle of the nineteenth century. This was preceded by a period of approximately 150 years in which there was no trend. The results that we have presented suggest that this trend is associated with a surface warming over western North America throughout the period for which we have good-quality surface data, 1870–2000. Furthermore, the Mount Logan time series is correlated with the PNA over the period for which we have good-quality information on its variability, 1925–2000. With respect to the PDO, there exists a statistically significant correlation only after the middle of the twentieth century. It therefore appears that the secular trend in the Mount Logan snow accumulation time series is associated with a long-term intensification of the PNA. Our analysis suggests that the PDO has undergone a similar intensification, but only since the middle of the twentieth century. Over the past 50 years, this relationship between the PNA and the PDO may have contributed to the observed rapid increase in snow accumulation at the Mount Logan site and the acceleration in the warming over northwestern North America. □

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Altered performance of forest pests under atmospheres enriched by CO_2 and O_3

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Human activity causes increasing background concentrations of the greenhouse gases CO_2 and O_3[1]. Increased levels of CO_2 can be found in all terrestrial ecosystems[2]. Damaging O_3 concentrations currently occur over 29% of the world's temperate and subpolar forests but are predicted to affect fully 60% by 2100 (ref. 3). Although individual effects of CO_2 and O_3 on vegetation have

been widely investigated, very little is known about their interaction, and long-term studies on mature trees and higher trophic levels are extremely rare[4]. Here we present evidence from the most widely distributed North American tree species[5], *Populus tremuloides*, showing that CO_2 and O_3, singly and in combination, affected productivity, physical and chemical leaf defences and, because of changes in plant quality, insect and disease populations. Our data show that feedbacks to plant growth from changes induced by CO_2 and O_3 in plant quality and pest performance are likely. Assessments of global change effects on forest ecosystems must therefore consider the interacting effects of CO_2 and O_3 on plant performance, as well as the implications of increased pest activity.

Atmospheric CO_2 concentrations have risen by nearly 30% since the mid-1800s (ref. 6), and background levels of tropospheric O_3 have risen concurrently from 10–15 $\mu l l^{-1}$ a century ago to 30–40 $\mu l l^{-1}$ today[7]. Controlled exposure of trees to CO_2 or O_3 drives plant responses in different directions, producing stimulatory (CO_2) or inhibitory (O_3) effects on aboveground growth[8]. Increases or decreases in substrate availability due to CO_2 and O_3 change metabolic use of growth-limiting resources such as light, water and nitrogen, and also alter the physical and chemical quality of plant tissues. In turn, such changes can affect the performance of higher trophic levels, particularly insects[9] and plant diseases[10]. Field-based investigations of the impacts of CO_2- and O_3-induced changes in tree quality on natural populations of pests and diseases have, however, only become possible since the development of free-air carbon dioxide enrichment (FACE) technology[11].

Here we report on the first free-air investigations into the impacts of increased CO_2 and O_3 on natural populations of forest insects and their natural enemies, and on natural outbreaks of tree diseases. The data we present link changes in physical and chemical plant defences with pest performance within the context of simultaneous treatment-induced changes to tree growth. To do this, we chose three model systems: one plant pathogen and two insects having widely different feeding strategies. The poplar leaf rust, *Melampsora medusae*, is common on aspen and belongs to the most widely occurring group of foliage diseases[12]. The forest tent caterpillar, *Malacosoma disstria*, is a common leaf-chewing lepidopteran in North American hardwood forests[13]. The sap-feeding aphid, *Chaitophorus stevensis*, infests aspen throughout its range[14].

Our data show that enhanced CO_2 and O_3 had no effect on trembling aspen tree height in 1998 or 1999, but that by 2000, with the onset of canopy closure, height growth began to diverge among

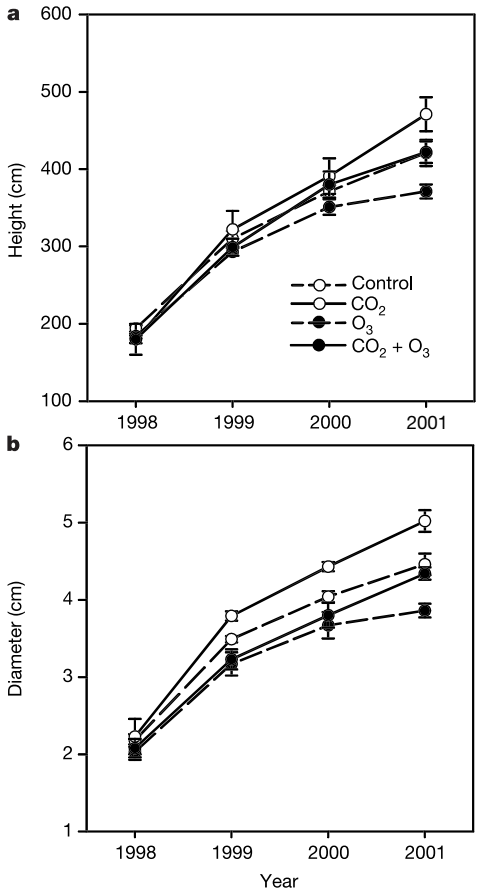

Figure 1 The effects of elevated CO_2 and O_3 on the growth of trembling aspen. Data are presented as means ± 1 s.e. **a**, We note the divergence of height due to treatment in year four of fumigation, the height stimulation due to CO_2 and the height depression due to O_3. **b**, Diameter growth due to treatment diverged earlier, after two years of fumigation.

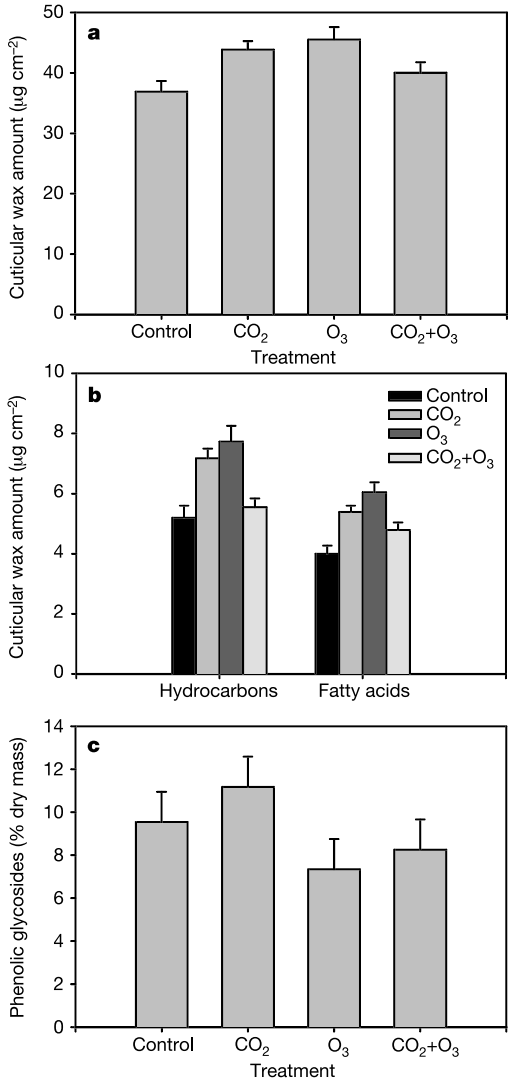

Figure 2 The effects of CO_2 and O_3 on physical and chemical leaf defences in trembling aspen. Data are presented as means ± 1 s.e. **a**, Comparison of amount of the physical barrier (cuticular wax) produced showing the contradictory influence of O_3 alone or in combination with CO_2. **b**, Comparison of carbon allocation among major cuticular wax classes known to act as phytophagous insect deterrents or stimulants. **c**, Concentrations of the important aspen defensive metabolites, phenolic glycosides (salicortin + tremulacin).

treatments (Fig. 1a). In 2001, four years after planting, trees grown in enhanced CO_2 were taller ($P = 0.005$), and those in enhanced O_3 were smaller ($P = 0.001$) than controls. Under $CO_2 + O_3$, the beneficial effects of CO_2 negated the adverse effects of O_3 ($P = 0.278$; Fig. 1a). Tree diameters, however, diverged almost immediately, and significant treatment effects continued through the 2001 growing season. Enhanced CO_2 increased tree diameter ($P < 0.06$), enhanced O_3 decreased it ($P < 0.06$) and trees with enhanced $CO_2 + O_3$ did not differ from the controls (Fig. 1b). These four-year data support our premise that, based upon a 2100 scenario for CO_2 and O_3, aspen growth, survival and productivity will be greatly affected by these two air pollutants[15]. The implications are huge because, since the mid-1990s, aspen use has increased almost exponentially in the US Great Lakes Region and in the boreal mixed wood region of Canada, where the resource is now almost fully utilized[16].

Because our tree performance data were gathered from a 'natural' ecosystem, we were able to monitor natural outbreaks of pests and diseases. We relate the impacts of CO_2 and O_3 on populations of insects and diseases to those on trees in the control rings (360 $\mu l\,l^{-1}$ CO_2; 36.0–38.8 $\mu l\,l^{-1}$ O_3 during the growing season (1998–2001) in the daytime (07:00–18:59) on average) because there are no 'pest-free' trees in our experiment.

We focused our initial effort on the leaf cuticle, an important defensive barrier against pests[17]. Exposure of aspen to enhanced CO_2 and/or O_3 greatly altered production ($P < 0.0001$) and chemistry

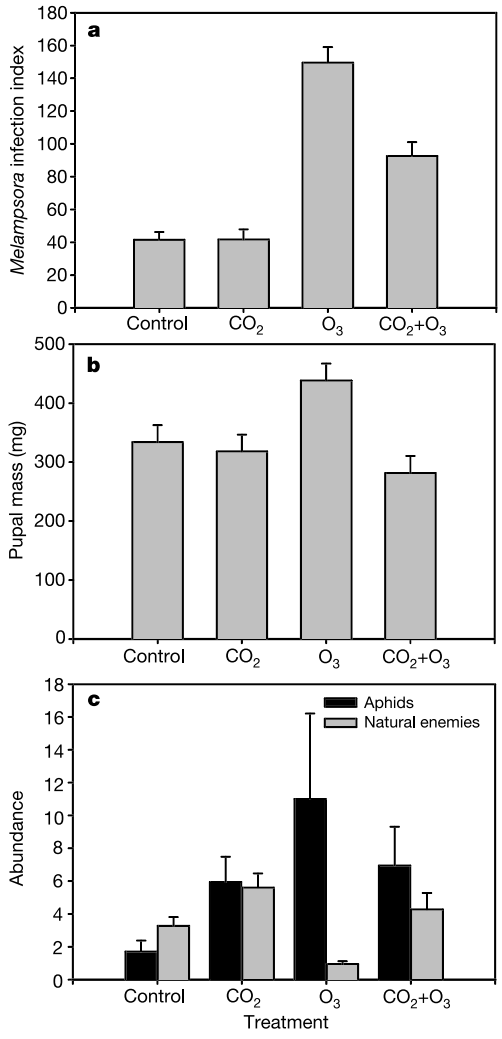

Figure 3 Effects of CO_2 and O_3 on one pathogen and two important herbivorous insects found on aspen **a**, *Melampsora medusae* infection; we note that rust increased on leaves exposed to O_3 relative to both the control and those exposed to CO_2 alone. A mid-range response was observed for leaves exposed to $CO_2 + O_3$. **b**, Performance of a lepidopteran, leaf-chewing insect, the forest tent caterpillar, as assessed by female pupal mass. We note the increased performance under O_3 and decreased performance under CO_2, especially under high O_3. **c**, Mean numbers of aphids and natural enemies (ladybirds, lacewings, spiders and parasitoids) per tree. Under O_3, sap-feeding aphid numbers increased while their natural enemies simultaneously decreased.

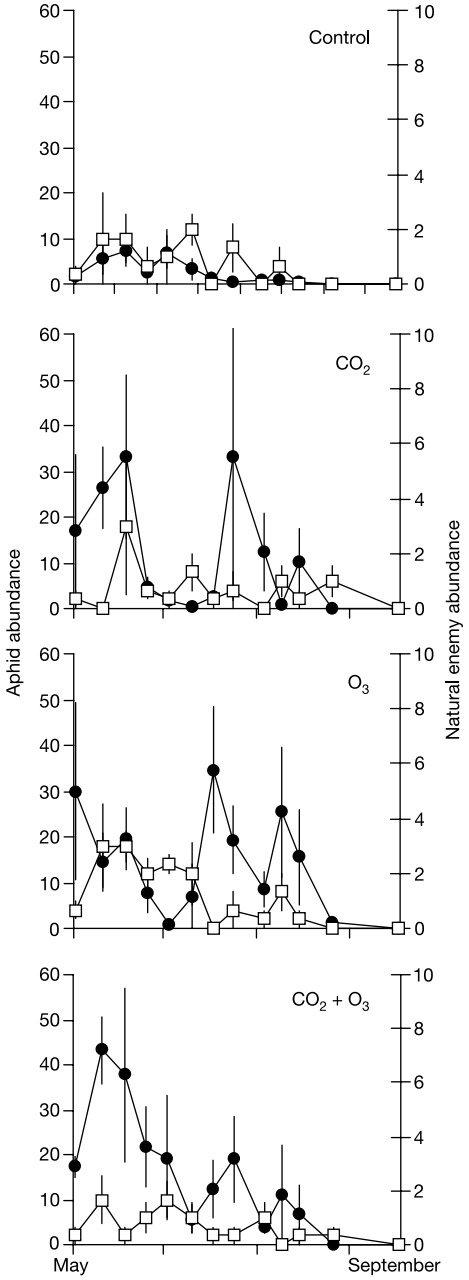

Figure 4 Long-term effects of enhanced CO_2 and O_3 atmospheres on the abundance of aphids (filled circles) and natural enemies (open squares) feeding on aspen. Aphid abundance increased significantly under elevated CO_2 and/or O_3, while natural enemy abundance did not, although we note changes in the patterns of natural enemy population increases.

($P < 0.001$) of cuticular waxes. Exposure to CO_2 or O_3 stimulated cuticular-wax production (16 and 23%, respectively) (Fig. 2a). Increasing C allocation to cuticular waxes owing to CO_2 ($P = 0.0029$) or O_3 ($P = 0.0021$), however, was negated under $CO_2 + O_3$ ($P = 0.215$) (Fig. 2a). Of particular relevance is that modifications to cuticular waxes determine the physicochemical characteristics of the plant surface on a scale relevant to plant-eating and insect-eating insects through action upon attachment, host location and host acceptance[18]. We show here that synthesis of fatty acids (which stimulate host recognition[18]) was increased by CO_2 ($P = 0.0001$) and O_3 ($P = 0.0001$) applied singly, as well as by $CO_2 + O_3$ ($P = 0.037$) (Fig. 2b). Coincidentally, both CO_2 ($P = 0.0002$) and O_3 ($P = 0.0002$) increased amounts of hydrocarbons (Fig. 2b), which are known to help insects recognize surfaces by increasing their responsiveness to chemical cues[18].

Changes to plant defences under enhanced CO_2 and O_3 also involve changes in the chemical composition of the leaf tissue. Trembling aspen accumulates high concentrations of phenolic glycosides, which are of singular importance as protective agents against pests[19]. Phenolic glycoside concentrations increased under enhanced CO_2 ($P = 0.046$), and decreased under enhanced O_3 ($P = 0.002$) (Fig. 2c). The independent effects of CO_2 and O_3 were attenuated when the trees were exposed to both gases simultaneously. As CO_2 and O_3 obviously induced changes to aspen physical and chemical defensive characteristics, we next investigated the impacts of these changes in host quality on performance of the insects and diseases naturally infesting our aspen trees.

The role of cuticular wax as a physical barrier to protect leaves from fungal infection is well established[20]. We have previously shown how O_3 alters aspen cuticular-wax structure and increases leaf wetting[21]; the latter is a function of the ratio of the most hydrophobic (hydrocarbons) to least (fatty acids) hydrophobic cuticular wax[22]. Rust infection increased fourfold under enhanced O_3 ($P < 0.001$, Fig. 3a). CO_2 alone did not alter rust occurrence. Interestingly, co-exposure did not completely offset the negative effects of O_3, as infection remained almost threefold increased compared with the control leaves ($P = 0.022$). As yield loss due to *Melampsora medusae* can lead to reduction in diameter growth and delayed development of root systems[23], we suggest that the negative effects of O_3 environments on aspen productivity in Aspen-FACE (Fig. 1) were due to the interacting stresses of O_3 toxicity and increased leaf damage by *M. medusae*.

Historically, the forest tent caterpillar has defoliated more deciduous forest than any other insect in North America and regularly defoliates large areas (up to 26×10^6 ha) of early successional forests[16]. Outbreaks can reduce timber yield up to 90% in one year, and increase tree vulnerability to disease and environmental stress[24]. Enhanced CO_2 ($P = 0.020$) reduced female pupal mass, particularly under high levels of O_3 ($CO_2 \times O_3$ interaction, $P = 0.046$) (Fig. 3b). In contrast, O_3 fumigation improved tent caterpillar performance, increasing female pupal mass by 31% ($P = 0.039$). As large forest tent caterpillars produce more offspring than small individuals[25], the increase in pupal mass due to O_3 suggests that future outbreaks of this important forest pest will be more severe (under higher O_3 environments) than at present.

Changes in forest tent caterpillar performance may also affect interactions with higher trophic levels, because natural enemy performance frequently depends on size and quality of the prey[9]. We chose aphids (and their natural enemies) for our population surveys of tritrophic interactions. Aphids were ideal for investigations of the impacts of CO_2 and O_3 on pest and natural enemy populations because aphids spend their entire life cycle on the trees in the FACE rings and the performance of multiple generations can be investigated during a single growing season. Population surveys revealed that, although aphid abundance was unaffected by CO_2 and O_3 (Fig. 3c), natural enemy densities were much larger ($P < 0.001$) under CO_2 than under the control treatment. In contrast, O_3 had a strong negative effect ($P = 0.002$) on natural enemies, but did not modify CO_2 effects ($P = 0.241$).

The long-term population surveys we conducted the following year showed that, despite the high variability associated with natural aphid infestations (a result of their exponential population growth rates), aphid abundance was, on average, significantly ($P = 0.0231$) greater on trees grown under enhanced O_3 than on control trees (Fig. 4). Peak aphid populations also increased on trees grown under enhanced CO_2; although in this case, the result was dependent on the sampling date and O_3 concentration (significant $CO_2 \times O_3 \times$ date interaction; $P = 0.019$). In this long-term study, enhanced CO_2 and O_3 had no overall effect on the abundance of natural enemies (averaged over the growing season), but did affect the synchrony of natural enemies with their aphid hosts (Fig. 4). The long-term investigation of the impacts of enhanced CO_2 and O_3 on the population dynamics of aphids and their natural enemies clearly shows that aphid infestations were more severe on trees grown under enhanced CO_2, O_3 or $CO_2 + O_3$ atmospheres. Aphid populations under enhanced CO_2 and O_3 did not reflect the performance of individual aphids (which was unaffected by CO_2 and O_3) or the effects of CO_2 and O_3 on the nutritional or defensive quality of the leaf tissues (Fig. 2c); as aphids are phloem-feeders, this was not surprising. The effects of CO_2 and O_3 on aphid abundance did, however, correlate well with the increase in plant cuticular wax (Fig. 2a, b) and also reflected trends observed for *M. medusae* (Fig. 3a).

Populus tremuloides and its close relative European aspen, *Populus tremula*, are worldwide species, and important components of many forest ecosystems[5]. Our report represents the first ecosystem-level description of the combined effects of enhanced CO_2 and O_3 on the relationship between food quality and the long-term population dynamics of major forest pests. Here, we have shown the potential for a multitrophic effect, albeit for selected plant defences and pest taxa, within an ecologically important forest ecosystem grown under realistic exposure to future CO_2 and O_3 concentrations. From our results, we believe it important to emphasize that: (1) studies of the performance of individual herbivorous insects would not have allowed us to predict the long-term population dynamics of pest and natural enemy populations; (2) although natural enemy abundance may be affected by changes in CO_2 and O_3, the long-term regulation of pest populations by natural enemies appears to be less effective under enhanced CO_2 and/or O_3; (3) changes in pest dynamics reflect changes in leaf defensive qualities, particularly aspects of leaf quality such as changes in 'host signalling' at the leaf surface, with wider implications for host 'acceptance' by other pest/pathogen species; and (4) feedbacks to tree productivity are likely now occurring or will ensue and may modify forest responses to increasing CO_2 and O_3.

In its Third Assessment Report, the IPCC stated that "...the increase of greenhouse gas concentrations in the atmosphere can be reduced also by enhanced uptake of carbon through, for example, afforestation, reforestation, slowing deforestation, and improved forest, rangeland, wetland, and cropland management..."[26]. Yet the degree to which terrestrial ecosystems will continue to be net sinks for carbon is highly uncertain, owing to the complex interactions among an array of natural and non-natural factors. We believe the assessments of carbon sequestration in woody biomass[27], without consideration of the importance of CO_2 and O_3 interactions and the potential for increases in populations of insects and diseases, will seriously overestimate the positive effects of enhanced CO_2 atmospheres on the productivity of northern forests. □

Methods

The experiment

The Aspen-FACE site (32 ha) is located on a level to gently rolling sandy loam in northern Wisconsin, near Rhinelander (longitude, 89.7°, latitude, 45.6°), well within the natural range of the dominant experimental species, trembling aspen, *Populus tremuloides*

Michx.[28]. The FACE system was constructed in 1997, and has been used to fumigate (1998–2001) developing forest stands. The experiment consists of 12, 30-m-diameter FACE rings, assigned to factorial treatments of atmospheric CO_2 (ambient and 560 $\mu l\,l^{-1}$ during daytime hours) and O_3 (ambient and 46.4 $\mu l\,l^{-1}$ to 55.5 $\mu l\,l^{-1}$ during the growing season (1998–2001) in the daytime (07:00–18:59) on average for the six O_3 treatment rings). The four treatments are arranged in a randomized complete block design, with three replications of each treatment. Each FACE ring is divided by a walkway system into three parts. In one half of each ring, we planted five trembling aspen genotypes of differing O_3 and CO_2 responsiveness. The other half of each ring is further divided into two quarters; one is planted with aspen and sugar maple, *Acer saccharum* Marsh., and the other is planted with aspen and paper birch, *Betula papyrifera* Marsh.; each FACE ring is planted at a 1 × 1 m spacing. In June 1997, 12,000 trees were planted inside the rings (1,000 trees per ring). The performance of our FACE exposure system, the growth responses of the trees and additional details of our experiment have been summarized in detail elsewhere[28].

Tree height and diameter measurement

Tree height and diameter were measured at the end of each growing season, after leaf fall. Tree height was assessed using a telescoping height pole and diameter was assessed at 3 cm above the soil surface along two axes, using callipers[15].

Plant assay methods

Cuticular waxes were recovered by chloroform washing from physiologically similar, fully expanded main lateral leaves collected from aspen trees growing within each ring. Wax amount (10 ± μg) was expressed in relation to leaf surface area and quantitative leaf cuticular wax chemical composition was determined using gas chromatography (GC) and GC-mass spectrometry (MS) as described elsewhere[29].

Positive identification of *Melampsora medusae* Thuem. F. sp. *tremuloidae* was confirmed by observations of urediniospores using scanning electron microscopy (SEM) and/or light microscopy. Rust incidence was assessed in late September as percentage of infected leaves per tree and severity of rust occurrence per leaf. Their product was calculated as the incidence of infection[10].

Invertebrate surveys

Leaves used for phenolic glycosides determinations were collected during the fourth larval instar of forest tent caterpillar development. Foliage (2–3 g fresh mass) was excised at the petiole from each tree, flash frozen in liquid nitrogen, freeze-dried, ground, and stored at −20 °C before analysis. Levels of the phenolic glycosides salicortin and tremulacin were measured using high-performance thin-layer chromatography (HPTLC), with purified aspen salicortin and tremulacin as reference standards[30]. Forest tent caterpillar larvae were reared communally in large mesh bags until the fourth instar, at which time they were placed in individual mesh bags (five larvae per tree, three trees per ring) and reared to pupation.

Total numbers of aphids and natural enemies on seven aspen trees from each ring were counted. Data were $\log_{10}(n + 1)$ transformed before analysis. No winged aphids were found on any of the trees; thus all aphids are likely to have been born and developed from the initial colonization of the trees by winged females early in the growing season. The natural enemies were mainly predators (such as Coleoptera and Neuroptera) and parasitic Hymenoptera. Although the data are likely to have underestimated the total number of natural enemies (particularly winged species) exploiting the aphid populations, they represent a snapshot of the population at the time of the survey. More comprehensive sampling (for example, by using insect traps) would have included natural enemies exploiting insects feeding on all the trees growing in the FACE rings, rather than aspen-feeding aphids. The long-term aphid and natural enemy population surveys used similar methods, except that data were collected from the lowest south-facing branch on each tree rather than from entire trees. In the previous survey, aspen aphids were found only on the lower branches; no aphids were ever found on the upper branches.

Statistical considerations

Data were analysed by general linear models analyses of variance (ANOVA). The Aspen-FACE experimental design, at the whole-plot (error d.f. = 6) level, is three replications of a randomized complete block design with four treatment combinations. We assume that replications are random effects, and treatments are fixed effects[28].

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Genetic mechanisms of floral trait correlations in a natural population

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Genetic correlations among traits are important in evolution, as they can constrain evolutionary change or reflect past selection for combinations of traits[1,2]. Constraints and integration depend on whether the correlations are caused by pleiotropy or linkage disequilibrium[3], but these genetic mechanisms underlying correlations remain largely unknown in natural populations[4]. Quan-

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erratum

Control, exploitation and tolerance of intracellular noise

Christopher V. Rao, Denise M. Wolf & Adam P. Arkin

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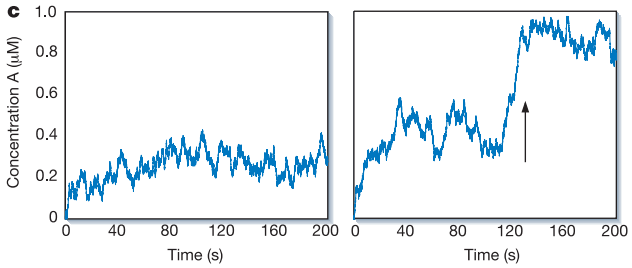
In this Insight Review Article, the right panel of Fig. 3c incorrectly appeared blank. Figure 3c should have appeared as shown:



corrigendum

Altered performance of forest pests under atmospheres enriched by CO_2 and O_3

Kevin E. Percy, Caroline S. Awmack, Richard L. Lindroth, Mark E. Kubiske, Brian J. Kopper, J. G. Isebrands, Kurt S. Pregitzer, George R. Hendrey, Richard E. Dickson, Donald R. Zak, Elina Oksanen, Jaak Sober, Richard Harrington & David F. Karnosky

Nature **420**, 403–407 (2002).

In this Letter, the conversion to SI units led to several errors. On page 404, left column, lines 16 and 17, the values should read 10–15 and 30–40 nanolitres per litre. On page 405, right column, lines 3 and 4, the values should read 360 microlitres per litre and 36.0–38.8 nanolitres per litre. On page 407, left column, lines 3 and 4, the values should read 560 microlitres per litre, and 46.4 to 55.5 nanolitres per litre. The conclusions of the paper are not affected. □