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Biochemical and Physiological Aspects

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Introduction

Forest ecosystems fulfill various functions with economic, social, and ecological significance. They also form habitat for various species of plants and animals. However, forest ecosystems are exposed to serious threats from attacks by parasites and diseases, from air pollution, fires, and climatic changes. As forests are sensitive ecosystems, they are susceptible to these disturbances, whether caused by biotic or abiotic influences. These biotic and abiotic influences could be of natural origin (such as fires, insect or pathogen attacks, and species invasion) or anthropogenically caused (such as air and soil pollution, global climatic changes, and fragmentation). In this article some physiological and biochemical aspects of tree responses and forest health will be reviewed. The contribution is focused on air pollution (in particular ozone) and climate change (in particular elevated atmospheric CO_2 concentrations) and how these relate to forest health. These two issues provide a good basis for understanding the links between biochemistry and physiology and forest health. So, the contribution is restricted to these two stress factors as they are used as examples of how trees respond to external stresses.

With regard to air pollution, various atmospheric pollutants might affect tree growth and forest health such as nitrogen dioxide (NO_2), nitrogen oxides (NO_x), ozone (O_3), sulfur dioxide (SO_2), hydrofluoride (HF_6), and hydrocarbons (such as CH_4). Air pollution can change the physical and chemical environment of forest trees. Pollutant stresses, as well as competitional, climatic and biological stresses, have important implications for forest growth and ecosystem succession because they provide forces that favor some genotypes, affect others adversely, and eliminate sensitive species that lack genetic diversity. Pollutant stresses in a forest ecosystem are superimposed upon and interact with the naturally occurring stresses that trees are already experiencing. These additional stresses can accelerate the processes of change already underway within ecosystems.

Forests and the human uses of forests and forest products have an impact on greenhouse gas concentrations in the atmosphere. There is a feedback from the climate system where forests are affected by the changes in climate, and the chemical composition of the atmosphere. Forest ecosystems and wood-based products also have the ability to sequester atmospheric CO_2 and thus offer an opportunity to mitigate climate change. However, this balance must be correctly understood, quantified, and modeled if we wish to assess the potential of forests to regulate sudden climatic changes, to improve the reliability predictions, and to reduce the uncertainty of the consequences of climatic change on forest health and forest ecosystems. As photosynthesis is the key process that all autotrophic organisms (trees, green plants, and algae) use to exchange mass and energy with the environment, this process will first be briefly reviewed.

Photosynthesis and the Importance of Nitrogen

Photosynthesis is the principal process to perform two essential transformation processes – on the one hand the conversion of high-quantity solar energy into high-quality chemically fixed energy, and on the other hand the conversion of simple inorganic molecules (CO_2, H_2O) into more complex organic molecules (sugars and carbohydrates). The harvestable product of a tree, generally the stem, depends not only on photosynthetic carbon uptake by the foliage, but also on respiration of the various organs and carbon investments into renewable organs (leaves, fine roots) and generally nonharvested organs (branches and large roots). Consequently, there is no obvious relationship between photosynthesis and wood production. A fast-growing tree generally needs high photosynthesis, but the reverse is not necessarily true. When growth is related to total net photosynthesis integrated over the entire growing season and the total light intercepting leaf area, positive relations are generally obtained. However, photosynthesis remains the principal physiological process that also closely reflects the response of a tree to abiotic or biotic disturbances.

Abiotic factors such as light, temperature, CO_2 concentration, vapor pressure deficit, and nutrient status, but also air pollution, climatic changes, and drought, have a major effect on net photosynthesis, and thus on tree growth and productivity. All environmental conditions that tend to reduce the photosynthetic rate (including low light, low temperature, low nutrient availability, and high air pollution levels) reduce the photosynthetic carbon gain. Plant water status and ozone level, for example, influence the carbon relations of a tree at the gas exchange and growth levels. Low nutrient uptake reduces the amount of nutrients available for incorporation into new living biomass. In particular, a shortage of phosphorus and nitrogen severely affects the photosynthetic capacity. In addition, the partitioning of carbohydrates will favor construction of a larger root biomass for nutrient uptake. All tree species appear to have a large degree of adaptability to the climatic conditions of their habitat at the photosynthesis level.

Nitrogen is required by trees (and all other plants) in large amounts. To a large extent, it governs the use of phosphorus, potassium, sulfur, and other nutrients. Approximately 75% of the nitrogen in a plant leaf is required for the photosynthetic machinery. In natural ecosystems, such as most forests, nitrogen is usually a growth-limiting factor. In mature forests, however, nitrogen demand can be low. Changes in the nitrogen supply of an ecosystem can have a considerable impact on its nutrient balance. Nitrogen saturation can mean that some other resource such as carbon, phosphorus or water, for example, rather than nitrogen, becomes the growth-limiting factor. There are pronounced differences in nitrogen content and in photosynthetic capacity per unit of nitrogen among tree leaves grown under different conditions of light (both quantity and quality), of soil nutrient content, and of atmospheric composition (CO_2 level, ozone concentration). Specific leaf area (i.e., the ratio of leaf area to leaf dry mass), nitrogen content, and photosynthetic quantum efficiency differ significantly among leaves grown under these various conditions.

Tree Responses to Air Pollution

General Effects of Air Pollution on Forest Health

The degree to which vital tree functions are affected by pollutants and the extent to which visible damage can be detected depend on many factors, both biotic and abiotic. The most important of these factors are the species, age, growth form, developmental phase, and general vigor of the plant, climatic and edaphic conditions, but also the chemical nature, concentration, time, and duration of action of the different pollutants. Air pollutants can act on trees in both chronic and acute ways. In several cases the effects of pollution are proportional to the product of the concentration of the air pollutants and the duration of exposure, but the relationship is only linear over a certain range. The lower limit of this range is set by the concentration threshold, below which there are no observable changes, even after prolonged exposure to pollution. At the upper limit of the range, i.e., when a certain high concentration is exceeded, even very brief exposures cause damage. The effect of pollutants also depends on the time of day when their concentrations are highest. Peak concentrations of atmospheric pollutions occurring before noon, when the stomata are usually fully open, are more harmful than if they occur during the night. On the other hand, if the trees have only been exposed to toxic fumigations (e.g., photooxidants) for a few hours during the day, the night can be a time for recovery.

The symptoms of damage are varied and usually nonspecific. The same pollutant may generate quite different effects in different species and, on the other hand, the same symptom may be produced by several different pollutants. The nature and intensity of damage caused by individual pollutants are modified by all other simultaneously active environmental and stress factors. Trees subjected to pollution suffer greater damage from drought and frost than healthy trees. Criteria for early warning of incipient pollution damage are: disturbances in photosynthesis and modified response of stomata, accumulation of pollutants in the tree, reduction of buffering capacity of tissues, reduced or enhanced activity of enzymes, appearance of stress hormones (especially ethylene), and increase or decrease of respiration activity. However, in order to evaluate a stress situation, conclusions cannot be drawn from certain symptoms alone, but response patterns based on more than one criterion should rather be considered.

Acute damages appear as erosions of epicuticular waxes on the surface of leaves or needles, e.g., as a consequence of acid effects; other acute damages due to toxic effects are chlorophyll leaching, discoloration of leaves, necrosis of tissue, dieback of shoots, or dying of the whole plant. Generally, damage of this kind only occurs in the immediate vicinity of the pollution source. Spatially restricted forest damage caused by inputs of high concentrations of sulfur dioxide (SO_2) and halogenides in the vicinity of smelting works and industrial plants is well known. On a larger scale, a decline in growth vigor and severe damage were observed in spruce forests of central Europe at the beginning of the 1970s. Supposedly, the far-reaching air pollution of sulfuric gases and the associated soil acidification due to depositions in those days were the main cause of the damage. Chronic damage leads to reduced productivity and defective fertility (e.g., pollen sterility). In trees, growth, especially cambial growth, decreases. Based on changes in the structure of the wood and on the analysis of annual tree rings, the progressive pollution injury can be tracked and dated. As a particular example the physiological and biochemical responses of trees to one specific air pollutant (ozone) will be reviewed and summarized.

The Impact of Ozone

Ozone (O_3) is formed by photodissociation of molar oxygen and by electrical discharges. Like other air pollutants, ozone can act on trees in both chronic and acute ways. In the latter case, episodes of short duration (e.g., half an hour) and rather high O_3 concentration (100 to above 200 nl l^{-1}) may cause sudden and irreversible, physiological and macroscopic injury. The proposed initial event is membrane destruction. Depending on the location and climate, such O_3 episodes may be rare events. However, at many sites in the northern hemisphere, the mean seasonal O_3 exposure over a long period is significantly enhanced above the preindustrial level. This type of ozone impact is termed chronic. Tree responses to chronic exposure can distinctly differ from those to acute impact, even though the accumulating O_3 doses may be similar. Contrasting with acute effects, responses to chronic impact may reflect acclimatization, i.e., metabolic regulation, to ozone stress, including enhanced defense and repair capacities, but also endogenous burst induction. Also, such effects may eventually become irreversible. Under most field scenarios, chronic rather than acute ozone regimes appear to be ecologically meaningful for the long-term development of trees. Therefore, experiments that have employed acute O_3 regimes may have little relevance for interpreting plant performance, in particular of long-lived plants, like trees, under the prevailing chronic ozone scenarios of given field sites.

There is evidence that ozone after passage through the stomata rapidly decomposes into secondary oxidative derivatives which themselves can be injurious to the metabolism and structure of leaves so that the concentration of ozone approaches zero in the intercellular space of the leaf mesophyll (**Figure 1**). The decay of ozone into reactive derivatives, unless already occurring during the diffusive influx process, largely occurs in the mesophyll apoplast which contains antioxidants like ascorbate that form the first line in oxidant defense. To the extent that O_3 or its derivatives reach the plasmalemma, they may link to receptors that can initiate oxidative burst reactions and programmed cell death, leading to local necroses as a means against spreading injury. Such defenses are mediated at the gene level through molecular signal chains, including the oxidative ozone derivatives, ethylene formation, as well as salicylic or jasmonic acid. As ozone hardly reaches the chloroplasts, molecular signaling is also suggested to induce the decline of chloroplasts (loss of pigments and Rubisco activity). The mechanistic nature of the receptors and signal chains has only partly been unraveled to date; however, it appears that the primary defense against O_3 is rather similar at the cellular level to responses elicited by biotic agents.

Physiological and Biochemical Defense Mechanisms

After an exposure to air pollutants such as ozone, reactive oxygen species (ROS) are primarily formed within the apoplastic fluid of tree leaves. This first reaction is similar for other external stressors (including enhanced ultraviolet B radiation and salinity stress). Most probably the antioxidative capacity within the apoplast of exposed leaves is of significant importance in determining the resistance of trees to air pollution. Therefore forest researchers, and in particular tree modelers, are eager to introduce this parameter in models describing the real ozone flux, for example. However, the apoplastic antioxidative capacity should be considered with caution as it is not entirely clear what the best parameter is to estimate this antioxidative capacity. Many apoplastic antioxidants in relation to ozone and other air pollutants have been reported in the literature and ascorbate has been mentioned the most in this regard. Indeed, experiments have indicated high reaction constants between ascorbate and, e.g., ozone, ROS and other radicals, but its relative antioxidative capacity *in vivo* is still largely unknown. Moreover, the decay of ozone through a direct reaction with cell wall ascorbate is not sufficient to explain the different degrees of ozone sensitivity of different tree species.

The capacity to scavenge ROS has been assigned to a wide variety of molecules other than ascorbate. Examples of low-molecular antioxidants are phenolics (such as ferulic acid, caffeic acid, catechol, syringic acid, and *p*-coumaric acid), polyamines, diketogulonate, and glutathione. The involvement of phenolic compounds in the sensitivity of poplar (*Populus*) to ozone has clearly been demonstrated: after a single pulse exposure of a resistant poplar clone there was a marked increase of phenolic compounds. Phenolics are present in the apoplastic fluid and play an important role in lignin biosynthesis. Lignin is a complex macromolecule that originates from the oxidative polymerization of cinnamyl alcohols as the principal monomeric units. The question remains: how efficient are phenolic acids, compared to ascorbate, in scavenging ROS? Generally, this question remains

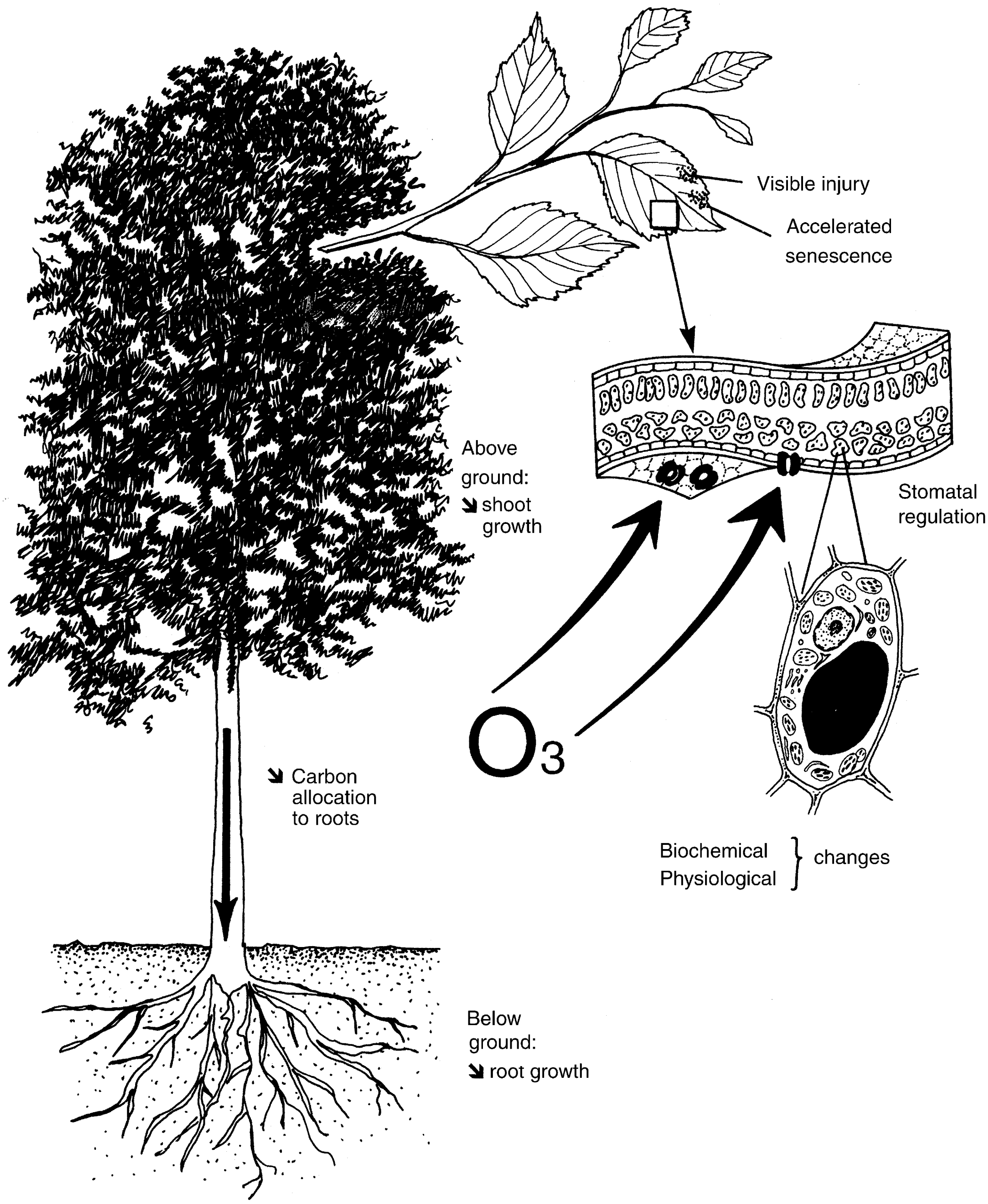

Figure 1 Schematic diagram of the impact of tropospheric ozone (O_3) on different physiological and biochemical processes at various hierarchical levels of organization. Ozone that enters the leaf through the stomatal pores alters different physiological and biochemical processes inside the leaf and the cells, but also affects a range of other functions and structures. *Environmental Pollution and Plant Responses* by Bortier K, Ceulemans R, and De Temmerman L. Copyright 1999 by CRC Press Inc. Reproduced with permission of CRC Press Inc.

unanswered, but a few naturally occurring components seem to have larger instantaneous antioxidative power than ascorbate (e.g., diketogulonate, ferulic acid, *p*-coumaric acid, gallic acid, resveratol, and quercetin). Because electronic transfer can take place between ascorbate and other antioxidants (e.g., phenolic acids), possible synergistic effects should be further considered in the future.

Climate Change Effects on Forest Trees

Role of Forests in the Global Carbon Cycle

In terms of carbon storage and cycling, forests represent the most important vegetation type on the earth. Although forests cover around 30% of the land area of the globe, they accomplish a disproportionately large part of the terrestrial bioproductivity

(65%), i.e., forests fix worldwide more or less 25 Gt of carbon per year. By their perennial character and longevity, forest ecosystems contain 80–90% of the above-ground plant carbon and 60–70% of the soil carbon on the globe. As such, they contain over 60% of the carbon stored in the terrestrial biosphere. So, forest ecosystems make up a stock of nearly 500 Gt of carbon in their biomass and a stock of nearly 700 Gt of carbon in the necromass, essentially under the form of organic matter in the soil. This impressive mass illustrates the buffering role that ecosystems can play in view of the additional carbon flux generated by the use of fossil fuels, by deforestation, and by changing land use. Apart from their significant role in the development of rural areas, forests have a major value for nature conservation, play an important role in preserving the environment, and represent a critical controlling factor of the hydrological cycle. However, forests are also key elements of the carbon cycle and represent significant carbon sinks.

The net carbon exchange of terrestrial ecosystems is the result of a delicate balance between uptake (photosynthesis) and losses (respiration and decomposition), and shows a strong diurnal, seasonal, and interannual variability. Under stable conditions, during daytime the net ecosystem flux is dominated by photosynthesis, while during the night, and for deciduous ecosystems in leafless periods, the system loses carbon by respiration. The total amount of carbohydrates produced in a forest canopy by photosynthetic carbon fixation is the gross primary productivity (GPP). Part of the produced carbohydrates is lost through autotrophic leaf respiration, while the rest is allocated from the leaves to other (tree) organs where it can be used for the construction of biomass or for metabolism and then respired as CO_2. The total amount of carbon incorporated in the biomass is the net primary productivity (NPP). The present atmospheric concentration of CO_2 limits the ability of forest trees to fix carbon. As tree photosynthesis is highly sensitive to atmospheric CO_2 and as NPP is strongly related to net photosynthesis, a stimulating effect of elevated CO_2 on NPP might be expected, provided that nutrient conditions are not limiting.

Tree Responses to Elevated Atmospheric CO_2

Because of the dependence of photosynthetic carbon fixation on the atmospheric CO_2 concentration, any increase in CO_2 tends to enhance the rate of assimilation and therefore plant growth. The reason why net photosynthesis may be enhanced is related to a number of factors connected to the characteristics of the primary carboxylating enzyme (i.e., Rubisco). Woody plants, when exposed to elevated CO_2 for varying periods of time, show not only stimulated photosynthesis, but also increased growth rate and biomass accumulation. Experiments on field-grown trees suggest a continued and consistent stimulation of photosynthesis of almost 40–60% for a doubling of the atmospheric CO_2 concentration and there is little evidence of a long-term loss of sensitivity to CO_2 that has been suggested by earlier experiments with tree seedlings in pots. Such an increase in photosynthesis translates into a 38% and 63% average increase in the biomass of coniferous and deciduous species, respectively. The relative effect of CO_2 on above-ground dry mass of field-grown trees is, however, highly variable and larger than that on seedlings or young saplings. Despite the importance of respiration to a tree's carbon budget, no strong scientific consensus has yet emerged concerning the potential direct or acclimation response of woody plant respiration to CO_2 enrichment. Effects of CO_2 concentration on static measures of response are often confounded with the acceleration of ontogeny observed in elevated CO_2.

A more robust and informative measure of tree growth in field experiments is the annual increment in wood mass per unit leaf area, which increases on average by 27% in elevated CO_2. There is no support for the conclusion from many studies of seedlings that root-to-shoot ratio is increased by elevated CO_2; the production of fine roots may be enhanced, but it is not clear that this response would persist in a forest. In general, nitrogen shortages are easily induced by accelerated growth in elevated CO_2, which could cause lower concentrations of nitrogen in leaves. Lower foliar nitrogen concentrations in CO_2-enriched trees result in larger attacks by herbivorous insects, an important contributor to fluxes of carbon and nitrogen in forest ecosystems. Experimental observations of lower nitrogen in leaves of trees grown in elevated CO_2 led to the suggestion that the behavior of herbivores feeding on those leaves is indeed affected. Although CO_2 effects on herbivory could have important ramifications for forest health, forest productivity, and nutrient cycling, there is not yet any framework for integrating the experimental observations with the population dynamics of the insect, as would be necessary for an assessment of the impact on ecosystem productivity.

Various climate models predict an increase in CO_2 emissions in the atmosphere and, simultaneously, an increase in the earth's temperature. Much of what we know about the contemporary global carbon budget has been learned from careful observations of the atmospheric CO_2 mixing ratio and the $^{13}C/^{12}C$ isotope ratio, interpreted with global circulation models. From these studies we have learned: (1) that about one-third of the annual input of CO_2 to the atmosphere from fossil fuel combustion and deforestation is taken up by the terrestrial biosphere; and (2) that a significant portion of the net uptake of CO_2 occurs at mid-latitudes of the northern hemisphere and that, in particular, north temperate terrestrial ecoystems (mainly forests) are implicated as a large sink. The method of stable isotope ratios combined with global circulation models provides the necessary global and continental scale perspectives for carbon balance calculations, but their use in addressing small temporal and spatial changes in the carbon balance is rather limited.

Over the last 200 years the flora of the earth has experienced a 28% rise in CO_2 concentration, having been progressively adapted to a CO_2-poor atmosphere for 20–30 million years. If current anthropogenic CO_2 emissions are not reduced and the rate of deforestation not slowed down, plants growing in the year 2040 will be exposed to around 500 ppmv CO_2, in contrast to the current levels of around 358 ppmv. The extent to which terrestrial ecosystems act as carbon sinks to buffer the increase in atmospheric CO_2 concentration (through enhanced NPP) is uncertain. However, the importance of forests and their interactions with climate are considerable, since trees account for nearly 65% of the terrestrial atmospheric CO_2 fixation. Their long life and large dimensions make them a considerable sink on carbon store on the earth. Evidence that past increases have directly affected trees is limited. Tree ring analysis and surveys of leaf chemical composition of leaves of herbarium specimens of 1750 AD revealed some important changes; the study of plant communities growing close to natural CO_2 sources has recently provided interesting and relevant information.

Actions to Monitor and Protect Forest Health

Worldwide actions have been and are being undertaken both to monitor and protect forest health. For example, European Community (EC) action has been developed over the years in cooperation with International Co-operative Programme on Assessment and Monitoring of Air Pollution Effects on Forests (ICP) and in line with objectives formulated in ministerial conferences on the protection of forests in Europe and the United Nations Conference on Environment and Development (UNCED, Rio de Janeiro, 1992). In January 2003 a proposal for a European Parliament and Council regulation (2003/C 20 E/10) was presented for the establishment of a new EC scheme on the monitoring of forests and environmental interactions to protect EC forests. The protection of forest ecosystems is a major concern to the EC. The main objective of the EC action is to contribute towards the protection of forest ecosystems in the EC by monitoring the conditions of these ecosystems. The EU and its member states are committed to the protection of forests and to the sustainable management of forests in all relevant pan-European and international processes related to forests. Forest ecosystem conditions, changes of these conditions, the reaction of forest ecosystems to environmental stress, and the effects of policies can only be traced by means of monitoring. Changes in forest ecosystem condition as well as the reasons for these changes may be recognized at an early stage, thereby allowing the adoption of timely and appropriate measures. The monitoring of air pollution and global change effects on forests will be carried out on a systematic network of observation points, which covers the whole Community, and a network of intensive monitoring plots. The systematic network provides representative information on forest conditions and changes. Intensive monitoring in selected plots allows for indepth monitoring activities in order to observe ecosystem processes. The intensive monitoring plots and the monitoring on the systematic network of points thus complement each other.

See also: **Environment**: Impacts of Air Pollution on Forest Ecosystems; Impacts of Elevated CO_2 and Climate Change. **Genetics and Genetic Resources**: Genetic Aspects of Air Pollution and Climate Change. **Health and Protection**: Integrated Pest Management Principles. **Tree Physiology**: A Whole Tree Perspective; Forests, Tree Physiology and Climate; Nutritional Physiology of Trees; Physiology and Silviculture; Stress.

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Integrated Pest Management Principles

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Introduction

Integrated pest management (IPM) has a variety of definitions, but its philosophy is simple. For a particular crop–pest interaction, one or more appropriate pest management tactics are combined into a package which minimizes costs and environmental impacts, whilst maximizing yields and net profits. Its two bedrock foundations are prevention and monitoring, i.e., strive to avoid pest problems at the outset, but keep a watch on the crop in case something significant goes wrong. IPM is a concept which is now widespread through all types of crop production, and it is increasingly the goal of any grower who loses yield, both quantity and quality, to damaging organisms such as weeds and nematodes, pathogens, and insects. As a practical crop protection solution, IPM is far from universal – it is often difficult, indeed sometimes impossible, to produce a viable IPM package. Problems which arise to curtail the full implementation of IPM include pest dynamics, host-plant and climate interactions, the practicalities of crop production, and very often, the socioeconomic conditions prevalent in the region of interest.

Forestry covers a very broad range of crop production tactics, from small-scale village forestry or agroforestry to huge plantations, either artificial or, at least initially, naturally occurring. Countries practicing forest management range from small, subsistence, isolated economies with little or no infrastructure to deliver education, specialist advice or spare cash to implement modern pest management protocols, to highly developed first-world countries to whom all the benefits of science and technology are theoretically available. Trees are grown from the furthest north and south temperate regions of the world to the equator, and from below sea-level to thousands of meters above sea-level. The trees themselves may be indigenous, native species growing in natural conditions to which they have evolved, or alternatively, they may be complete exotics with not even members of the family growing as natives in the locale, planted on sites which bear little or no relation to the conditions to which these trees evolved thousands of miles away. Nevertheless, many forestry practices and their associated pests and diseases have basic similarities, principles, and interactions, wherever in the world they occur.

In this section, insect pests will be discussed, but it must be borne in mind that many of the principles and indeed examples presented have a great deal of relevance to other forest pest situations, fungal diseases in particular. In fact, the modern approach to forest pest management is frequently not to target particular pests or diseases at the outset, but instead to employ the concept of general plant health and thus consider the widest range of symptoms and their underlying causes for tree decline and debilitation.

Insect Pests and Their Impacts

It is extremely helpful to consider trees as but one part in a complex ecology which has evolved over millions of years. Other crucial members of this association are at one end of the spectrum the environment in which the tree is growing (soil, climate, altitude), and at the other end, insects and diseases which utilize the tree for food or living space (or usually both). These herbivores themselves often have their own enemies in the form of predators, parasites, and pathogens, and the forester is simply one of these competitors for the resources which the tree provides. Unfortunately, this competition is very one-sided, especially in economic terms, since foresters cannot tolerate much, if any, resource removal by others – pests and diseases have to be defeated.

Paramount in this war to defeat the competition is the concept of impact. The actual harm done to a tree by an insect is frequently very difficult to assess. Heavy leaf loss may not be extreme when averaged over the life of the tree, especially when the trees are grown for many decades, whereas boring in the