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Environmental Pollution 137 (2005) 455–465

ENVIRONMENTAL POLLUTION

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Diagnosis of abiotic and biotic stress factors using the visible symptoms in foliage

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Received 10 December 2004; accepted 31 January 2005

The morphology and distribution of visible stress symptoms in tree foliage provides diagnostic tools to identify plant defense responses and differentiate stress from natural senescence symptoms.

Abstract

Visible symptoms in the foliage of trees are recorded to monitor the effects of abiotic and biotic stress. Difficulties are reported in diagnosing the origin of stress. The present paper discusses several diagnostic criteria which are usable in different species for a better determination of the stress factor type. A new diagnosis scheme to differentiate between classes of abiotic and biotic stress factors is supplied. Abiotic stress generates gradients of symptoms. The symptom specificity is determined by the degree of interaction between the stress factor and plant defense system. Symptoms caused by abiotic stress and natural autumnal senescence can be morphologically different or undistinguishable according to the stress and plant species. With biotic stress, the class of parasitic is generally recognizable on the basis of the visible symptoms. Structurally and physiologically based explanations of the symptom morphology are still missing for many stress factors.

Keywords: Diagnostic pathology; Broadleaved and conifer trees; Leaf coloration; Visible symptom expression; Stippling

1. Introduction

1.1. Visible symptoms in the foliage

Visible symptoms in the foliage of broadleaved and conifer tree species play an important role in detecting and scaling up the effects of various stress factors. Symptom descriptions are available in comprehensive textbooks (Altenkirch et al., 2002; Nienhaus et al., 1996; Hartmann et al., 1995; Skelly et al., 1990), specialized monographs (Innes et al., 2001; Hanisch and Kilz, 1990; Sinclair et al., 1987), articles (Vollenweider et al., 2003; Günthardt-Goerg, 2001; Günthardt-Goerg and Vollenweider, 2001) or websites (http://www.gva.es/ceam/ICP-forests/; http://www.ozone.wsl.ch/index-en.ehtml), but are often limited to the symptom morphology in the foliage. Many articles about stress physiology describe visible symptoms, but frequently only roughly and with insufficient illustrations. The attribution of a given symptom to a specific stress factor remains difficult despite the available literature. Consequently, visible symptoms frequently require further validation with microscopic analyses (Reig-Arminana et al., 2004; Vollenweider et al., 2003) or experimental tests in controlled conditions (Günthardt-Goerg and Vollenweider, 2003; Novak et al., 2003; Evans et al., 1996).

There are many difficulties associated with interpreting visible symptoms, several of which could be

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doi:10.1016/j.envpol.2005.01.032

remedied. As shown with ozone (Vollenweider et al., 2003; Innes et al., 2001; Skelly et al., 1990), the visible symptoms caused by a given stress factor may vary significantly between different species. With most other abiotic stress factors, however, only a few visible symptom descriptions are available to compare the symptoms displayed by different species. Stress factors may cause unspecific symptoms in foliage especially if the effects are indirect, as shown in the case of substrate contamination with Cd (di Toppi and Gabbrielli, 1999). Diagnosis is also complicated by the vanishing of biotic remnants with time and the interaction between stress factors resulting in different and simultaneously occurring symptoms in the same organ. Observer-related causes of confusion are lessening the efficiency of symptom diagnosis in several ways. They are often due to (1) limited understanding of how the analyzed stress factor impairs the leaf physiology and triggers the visible symptoms, (2) the ignorance of how specific the displayed symptoms compared to the natural autumnal discoloration patterns are, (3) the insufficient observation of the symptom distribution at tree, branch and foliage level, and (4) insufficient attention paid to symptom details. Increasing the skills of the observer thus represents an important potential for significantly improving the diagnosis efficiency.

1.2. Objectives

The present paper discusses several diagnostic criteria which can be applied to different species to better determine the type of stress factor. The objectives include (1) understanding the link between effects of stress and the symptom morphology and distribution, (2) showing that background knowledge about natural senescence symptoms during autumn is useful for the diagnosis of stress factor effects, and (3) comparing the symptoms displayed by different stress factors (bioindication). After introducing a diagnosis scheme, characteristic features in symptoms resulting from abiotic/biotic stress or natural autumnal senescence are compared.

2. Concerns

2.1. Identifying the stress origin of symptoms

Both the physiological changes and localization of tissue reactions following a given stress determine the resulting appearance of visible symptoms. For example oxidative stress, which can be found with ozone (Vollenweider et al., 2003), heavy metal (Günthardt-Goerg and Vollenweider, 2003) or drought (Munné-Bosch and Peñuelas, 2004; Noctor et al., 2002; Pääkkönen et al., 1998), causes characteristic and in several ways similar biochemical changes (Polle, 1997). The tannin content for example can be raised so much that it finally contributes to the visible expression of brownish hues (Vollenweider et al., 2003). In foliage, depending on the plant reactions and penetration ways of the stress signals (Günthardt-Goerg et al., 2003), such stress markers can be concentrated in characteristic areas of mesophyll or preferentially allocated near veins. They will consequently determine recognizable gradients in the visible symptom distribution in the foliage organ (Cosio, 2004).

The relative distribution of symptoms at the leaf, branch and crown level provides a basic indication to identify the class of stress factor. Indeed, an important difference between abiotic and biotic stress is that the first will affect the whole plant and often other plants and species growing nearby too (see Vollenweider et al., 2003 for examples with ozone stress). The symptom distribution varies according to foliage exposure, species and foliage physiological characteristics and consequently, symptoms are expressed along gradients. In contrast, in the case of a moderate biotic infection, the distribution of the affected foliage is more random depending on which crown part was first colonized. This differentiation therefore forms the first step in the diagnosis scheme proposed in Fig. 1. Abiotic stress factors may be further separated between those with an airborne and those with a soilborne origin. Shading effects, as shown by changes in symptom intensity, are reflecting differences in the crown's physical conditions (light, temperature) interacting with airborne stress, as found with drought (Fig. 2A,L,M), frost caused by drop in the air temperature (Hartmann et al., 1995), or ozone (Fig. 2B). With heavy metal contaminated soil, light exposure gradients are not observed (Fig. 2C) and the necroses are frequently connected to leaf veins (not shown). Biotic stress factors can be best identified, once the absence of gradients has been established, by directly detecting either the remnants or the parasite itself (Fig. 3E–H,L–M). After identifying a class of stress factors, a restricted number of stress origins remain as a potential cause for the symptoms observed (Fig. 1). The diagnosis then focuses on the leaf symptom morphology (Fig. 3A–H) and the sample and site history to finally determine the symptom cause. A stress factor can have both airborne and soilborne stress characteristics (Fig. 1). For example drought symptoms, following reduced precipitation (Figs. 2A,L,M and 3K) can show airborne (symptoms in the sun-exposed foliage/similar symptoms in other species at the same site/shading effects) and soilborne (symptoms connected to veins) features, as drought stress directly and indirectly affects several organs in the plant. The visible symptoms listed in Fig. 1 will be combined in the case of multiple stress effects. Diagnosis of stress symptoms is made easier in late summer because of the better

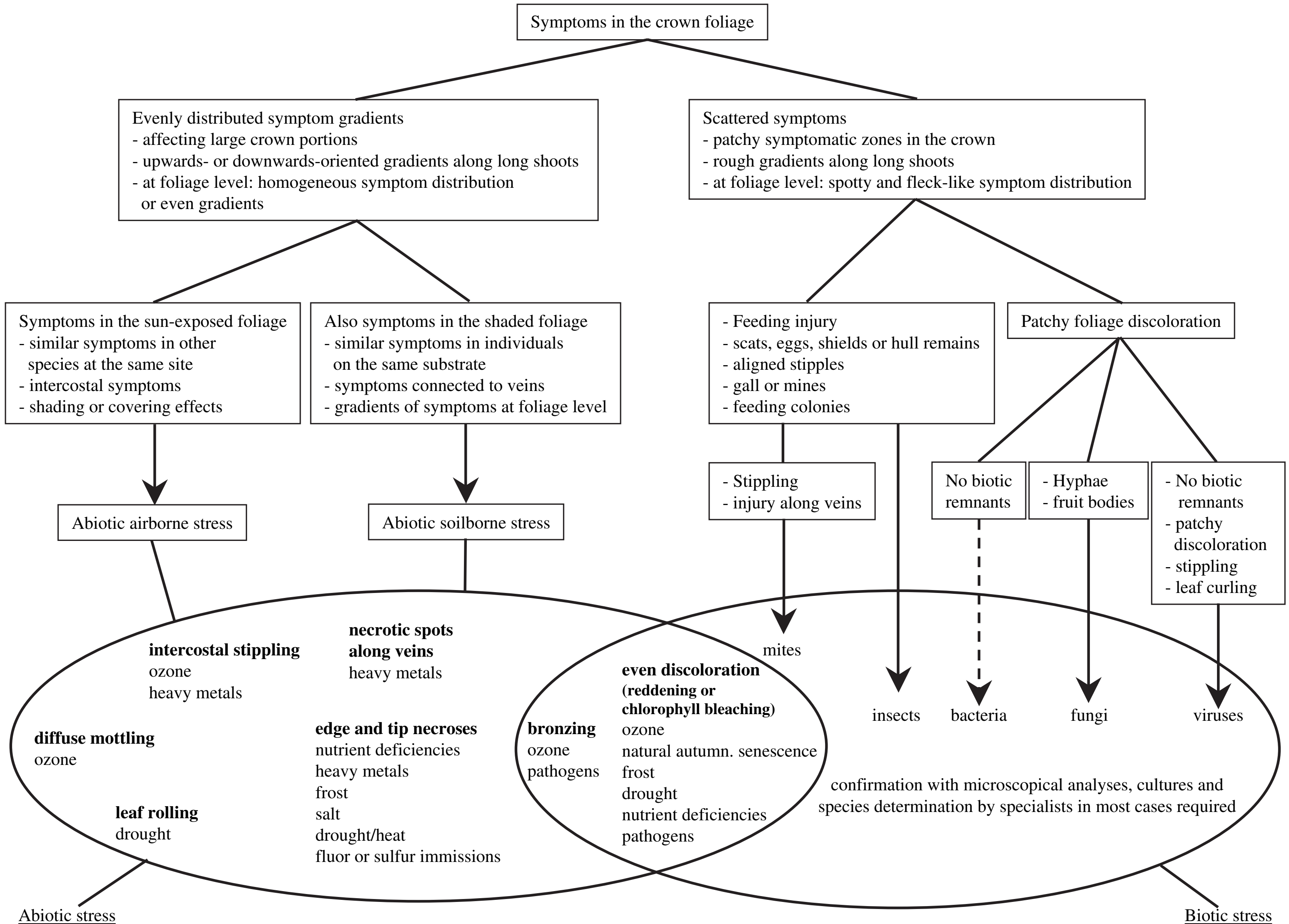


Fig. 1. Diagnosis flow chart for the identification of visible symptom types in the foliage. Application range: deciduous bush and tree species from central Europe, but also usable for conifers in the same temperate zone. The arrows in the model indicate the class of stress factors causing the visible symptoms, on the basis of the symptom morphology in the foliage and the symptom distribution and frequency at the foliage, branch and crown level.

Fig. 2. Differential symptom expression at the tree (A–G,J) and branch (H,I, K–M) level. Symptoms caused by abiotic stress factors are expressed along even gradients (arrow direction shows symptom intensity). At tree level, airborne stress like drought (A) or ozone (B) preferentially causes symptoms on the better light-exposed foliage as shown by brown hues in the light exposed foliage (detail in A: drought symptoms in leaves). (C) Soilborne stress, like heavy metal contamination, causes symptoms independently of the light exposure. (D) Symptoms with a biotic origin as with fungi (*) or mite (°) infection are scattered or follow rough gradients. Natural autumnal senescence (E–H,J,K) follows species-specific patterns. In large tree crowns, foliage discoloration can proceed homogeneously (F) or first start in the upper crown (G). In branches and young trees, autumn coloration develops along acropetally (E,J) or basipetally oriented (H) gradients. (K) Shading delays reddening in senescing leaves (* in comparison to detail). (L,M) Drought- and heat-induced gradients increasing with needle age (M) and lower leaf position (L). Bronzing gradient induced by ozone stress (upper branch in I) follows an opposite direction to that observed with natural autumnal senescence (H). Plant species: (A) *Alnus viridis*; (B,G,H,I,L) *Fagus sylvatica*; (C,D) *Populus tremula*; (E) *Larix decidua*; (F) *Quercus robur*; (J) *Sorbus torminalis*; (K) *Parthenocissus tricuspidata*; (M) *Picea abies*. Symptoms were observed in plants under field (A,B,E–M), or controlled experimental conditions (C,D). Field material grew in the sub-mountain (A,C–E,I–M), mountain (B) or hill (F–H) vegetation zones of Switzerland.

expression; however, it becomes frequently complicated by the effects of multiple stress, as shown in Fig. 3E. Consequently, the diagnosis of stress factors requires a deductive approach.

2.2. Natural autumnal senescence

Several stress factors accelerate the physiological evolution leading to foliage senescence (Munné-Bosch and Alegre, 2004; Pell et al., 1999; Baker and Allen, 1996). The resulting visible symptoms may look similar to those displayed during natural autumnal senescence; the only difference being the date which the symptom appears (earlier in the case of stress-accelerated foliage senescence). An example of such similarities is given by *Parthenocissus* with symptoms following ozone stress (Innes et al., 2001): the resulting whole leaf reddening cannot be differentiated from that occurring during natural autumnal senescence (Fig. 2K) except by the date when the symptoms become visible. The same is true concerning species like *Rubus fruticosus* or *caesius* (authors' observations). A background knowledge of how visible symptoms look during natural autumnal senescence or following needle aging is thus required to distinguish between stress-specific and accelerated senescence reactions. Unfortunately, relatively few publications are available on the subject of natural autumnal senescence. Among recent references, one concerns coloration development at crown level (Koike, 1990), six at leaf level (Lee et al., 2003; Schaberg et al., 2003; Matile, 2000; Merzlyak and Gitelson, 1995; Eschrich, 1995; Dean et al., 1993) and three plant/insect interactions (Archetti, 2000; Archetti and Brown, 2004; Hagen et al., 2003).

Koike (1990) established that in Japanese tree crowns the leaf coloration during autumn proceeded acropetally (inner type) or basipetally (outer-type), depending on species. These two coloration patterns also exist in other deciduous trees of the temperate zone as shown in Table 1 with several central European and one North American species (*Quercus rubra*). In Japan, the acropetal (or inner type) group includes early and the basipetal (outer type) late successional species. Early successional are also shade intolerant and late successional shade tolerant (Lyr et al., 1992). In the basipetal group of Table 1, *Fagus sylvatica* is a shade-tolerant tree (Lyr et al., 1992), *Quercus rubra* a middle successional species from North America (Chapman and Gower, 1991) (and a cultivated exotic species in Europe) and *Alnus viridis* a rather shade tolerant species (forming a bushy vegetation belt above the subalpine conifer forest; Ellenberg, 1996). Although Table 1 only shows a few examples, there could be more acropetal than basipetal types of tree species in central Europe. Acropetal and basipetal types determine the coloration patterns at branch and tree level in young plants, as shown in Fig. 2E,H,J,K). In large trees, other patterns can also be found (Table 1; Fig. 2F,G). Indeed, acropetal-type species like *Betula pendula*, *Larix decidua* or *Quercus robur* show a synchronous coloration development over most of the crown (Fig. 2F). Other acropetal- and basipetal-type species show a leaf color development first in their outer crown, progressing then to the deeper crown parts (Fig. 2G). In the case of an acropetal type such as the European *Acer* sp., the leaves at the tip color after those at the basis of shoot. Differences in each species' sensitivity to the temperature gradients inside a large crown might explain the differences in the coloration patterns.

Table 1
Type of leaf coloration development in different deciduous bush and tree species during the natural autumnal senescence

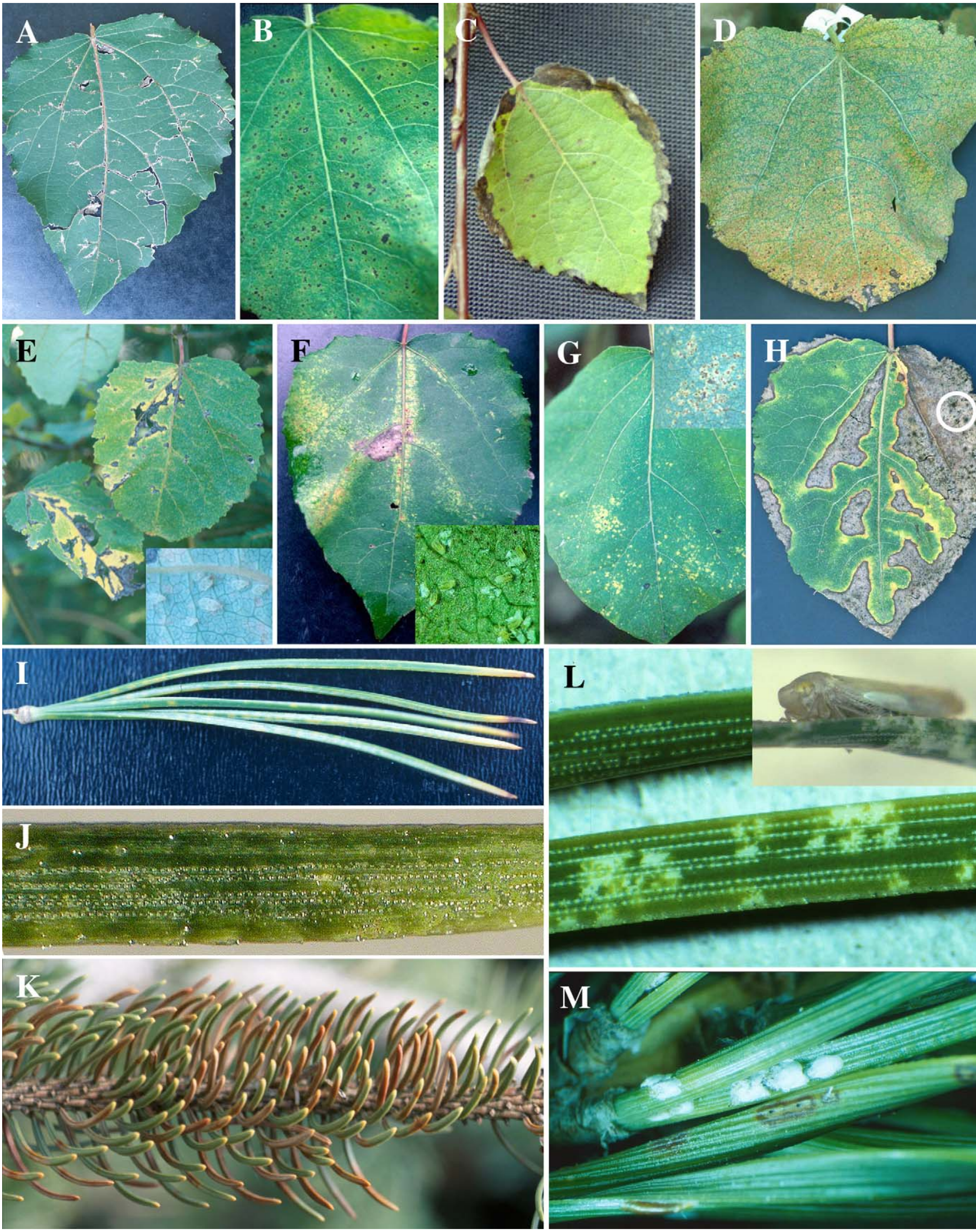
Basipetal	Acropetal
Alnus viridis[l]	*Acer platanoides*[l,v,b]
Fagus sylvatica[l,b]	*Acer pseudoplatanus*[l,v,b]
Quercus rubra[l,b]	*Betula pendula*[l,v,a]
	Carpinus betulus[v]
	Cornus mas[l]
	Corylus avellana[l,v]
	Larix decidua[a]
	Lonicera xylosteum[l]
	Populus tremula[l]
	Quercus robur[l]
	Salix aurita[l]
	Sorbus aucuparia[v]
	Sorbus torminalis[l]
	Viburnum lantana[l]

Leaves are coloring first at the tip of the shoots in the basipetal type and at the yearly shoot increment basis in the acropetal category. Categories are based on repeated observations of different cultivated or spontaneous specimens in the sub-mountain vegetation zone of the Swiss Plateau. In such conditions (500–800 m a.s.l.), the natural autumnal senescence generally starts in early October and is completed around one month later with a few weeks difference according to species and sites. Color development in foliage: [l]limb colors first, [v]veins color first.

[a] Simultaneous coloration of the whole tree crown.

[b] Coloration starts in the exposed portions of the tree crown.

Coloration gradients at the leaf level are indicative of the underlying physiological changes. Eschrich (1995) explains that progressive intercostal yellowing (Fig. 2H) is related to the orderly recycling of macronutrients through the phloem during autumn. However, vein prior to intercostal yellowing also occurs in several species (Table 1), without a valid explanation until now. Matile (2000) considers leaf senescence as a developmental process. This orderly reallocation of mineral elements results in even limb discoloration (Fig. 2H,J,K), which differs from patchy and stress-related color changes (Figs. 1 and 3B,D–H). Leaf reddening with vacuolar anthocyanins prior to chlorophyll degradation occurs in numerous species (Lee et al., 2003; Matile, 2000; Fig. 2J,K). Anthocyanins are light-intercepting pigments, they are inlayed in cells in the upper leaf blade layers (not shown) and are regarded as defense


A
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compounds (Dixon and Paiva, 1995). Onset and development of this red color in the leaf seems to correlate with a lower nitrogen and higher sugar content (Lee et al., 2003; Schaberg et al., 2003). Shading of leaf areas by other leaves (* in Fig. 2K) can delay the de novo synthesis (Matile, 2000) of anthocyanins during autumn (Fig. 2K), or following ozone stress. Yellow colors indicate the retention of carotenoids in the chloroplasts subsequent to the chlorophyll degradation (Lee et al., 2003; Matile, 2000).

2.3. Comparison of symptom traits caused by abiotic stress factors

Necrotic areas bordered by green tissues are typically abiotic and are observed by stress like drought (Figs. 2A,L,M and 3K), frost (Hartmann et al., 1995), hail (Fig. 3A) chilling (Fig. 3B) or sea salt spray (Fig. 3C). The structural changes in tissues remain poorly documented until now for several of these stress factors. At branch level, symptoms can develop acropetally (drought, Fig. 2C; chilling, not shown) or basipetally (frost, hail and sea salt spray, not shown). At foliage level, symptoms often look similar between different species for a given stress factor. With a mechanical injury, as shown here with hail (Fig. 3A), necroses are limited to the directly exposed zones in the fractured tissues. Leaf edge and tip necroses (Figs. 2L, 3C,D and 4) are observed in the case of different abiotic stress factors (Fig. 1). They all result from the disturbance in water and mineral element nutrition. The underlying, and maybe shared physiological and structural causes, remain unknown.

A few abiotic stress factors are interfering deeply with the plant defense system (Dietz et al., 1999; Schraudner et al., 1996), triggering different plant responses and causing programmed cell death (Günthardt-Goerg and Vollenweider, 2003; Vollenweider et al., 2003). The visible symptoms displayed are often highly stress- and species-specific (Figs. 2I, 3D and 4). With ozone in broadleaved species for example, many different symptoms can be found (Innes et al., 2001), with a more or less fine stippling (not shown) and different leaf discoloration (Fig. 2I), according to the species. In different species of pine, characteristic symptoms include mottling (Fig. 3I,J), and mesophyll discoloration (Dalstein et al., 2002). Plant responses underlying the visible symptoms are, however, less variable than the symptoms themselves and provide useful criteria for symptom validation by microscopy (Kivimäenpää et al., 2004; Reig-Arminana et al., 2004; Vollenweider et al., 2003). Some visible symptoms can be clearly attributed to these plant responses and thus become reliable diagnostic tools. Small necrotic dots, (1) uniformly scattered in the foliage, (2) generally visible with a hand lens only and (3) more or less outlined by the accumulation of anthocyanins or tannins in deciduous tree leaves (Fig. 3D) or with a diffuse appearance in conifers (Fig. 3I,J) often indicate a hypersensitive response (HR-like) triggered by an abiotic stress factor (Günthardt-Goerg and Vollenweider, 2003; Vollenweider et al., 2003). Besides ozone, different heavy metals like Zn can also cause such reactions in leaves (Fig. 3D). The associated local or total leaf discoloration (Fig. 2I) result from the enhanced senescence and oxidative stress in the nearby cells. In the case of stronger reactions, large necrotic areas can develop (Innes et al., 2001) which can be more difficult to distinguish at the visible symptom level than from other abiotically induced necroses without a HR-like origin (Fig. 3B,C).

The period of the year during which a visible symptom appears can provide a decisive diagnostic tool. Frost effects on perennials and new sprouts, or hail injury (Fig. 3A), are easily related to their cause—an extreme climatic event. Lasting unfavorable climatic conditions during spring can cause abiotic injuries (Fig. 3B) requiring laboratory analyses to be correctly diagnosed (not shown). An abiotic symptom where the intensity increases during the vegetation period signals accumulative stress. It is the case with drought (Figs. 2A,L,M and 3K), ozone (Figs. 2I and 3I,J) or heavy metal stress (Figs. 2C and 3D). Symptoms can be observed until late summer and their full development (Fig. 4) without confusion between stress-accelerated and natural autumnal senescence. An example of which is given in Fig. 4 for young uncoppiced poplar (*Populus tremula*) trees growing on experimentally contaminated soil (Zn 2700 ppm, Cu 385 ppm, Pb 63 ppm, Cd 10ppm). Symptoms were mainly induced by Zn as indicated by cytochemical localization and leaf metal content (not shown) and by the highly significant correlation found between the metal content and symptom intensity at the end of the vegetation season ($P<0.001$, $R^2=0.60$). Quickly developing stipples

Fig. 3. Variability of abiotic (A–D,I–K) and biotic (E–H,L–M) symptoms in one broadleaved tree (A–H) and different conifer species (I–M). (A) Mechanical injury in the leaf following hail. (B) Scattered necrotic dots surrounded by patchy chlorotic flecks following wet and cold spring periods (chilling stress). (C) Light chlorosis and necroses along edges following exposure to sea salt spray. (D) Adaxial stippling and spot necroses along edges following soil contamination with heavy metals and importation of Zn into the leaves. (E) Chlorotic areas on a hailed leaf following aphid (detail) sucking. (F) Adaxial stipples along veins signaling mite colonies (detail). Fungal infection with *Melampsora* sp. (G) and *Cladosporium* sp. (H); circle and detail (G): fruit bodies. Diffuse mottling caused by experimental (I) and field (J) exposure to ozone stress. (K) Needle browning due to drought stress. (L, M) Insect injury. (L) Irregular whitish spots following sucking by mesophyll-feeding cicadas (Cicadellidae, Typhlocybinae; detail: *Aguriahana germari*; Günthardt and Günthardt, 1983); (M) scale insects with waxy shields. Parasites in (E–G) were visible on the leaf lower side. Plant species: (A–H) *Populus tremula*; (I,J) *Pinus cembra*; (K) *Picea abies*; (L) *Pinus mugo*; (M) *Pinus sylvestris*. Leaf and needle material was collected in plants under controlled experimental (A,B,D–I,L) or field conditions (C,J,K,M). Field material grew on the northern German sea coast (C), in the subalpine vegetation zone of the French southern Alps (J) or in the sub-mountain (K) and hill (M) vegetation zones in Switzerland.

appeared about 1 month after budbreak on the leaves which first emerged. Symptom development was then slower with progressive leaf yellowing showing an acceleration of senescence. The first stippling thus occurred before the accumulation of sizable amounts of Zn. This suggests that the signal induced by the presence of the metal rather than the metal accumulation itself was the trigger for the HR-like reaction displayed. Similar patterns of development are also observed after exposure to ozone (Novak et al., 2003; VanderHeyden et al., 2001).

Symptom gradients along the branch also give valuable information. With ozone stress, for example, the most symptomatic leaves are always at the basis of shoots, even in species such as beech (*Fagus sylvatica*) with a basipetal senescence pattern (Fig. 2I vs. H). In conifers, exposure gradients exist at the needle level between the sky- and the soil-oriented side (Sutinen et al., 1990), a sure indication that ozone symptoms result from the interaction of both light and ozone stress (Vollenweider et al., 2003; Dalstein et al., 2002). With other accumulative stress, e.g. drought (Fig. 2A,L,M) and heavy metals (Fig. 2C), symptom development also proceeds acropetally.

2.4. Diagnosis traits to identify a class of biotic stress agents

Besides remnants and direct evidences, changes in the leaf and needle morphology are also useful to identify a biotic stress agent. If the stress symptoms are restricted to whitish dots or brown thread-like discolorations, they may indicate local necroses caused by micro-herbivory activity. More or less aligned white dots are generally caused by mesophyll-sucking small cicadas (*Aguriahana* in detail of Fig. 3L) in broadleaved and conifer trees. These insects completely suck out the cell content, with single probing during which insects feed along forked feeding paths. Therefore no defense reactions are observed in the surrounding mesophyll, except in a few cells adjacent to the sucking trace (Günthardt and Wanner, 1981). With phloem-sucking aphids (detail in Fig. 3E), a patchy acceleration of the leaf senescence (Fig. 3E) is frequently observed in the infested zone. As the phloem is a stress sensitive tissue (Matyssek et al., 2002; Günthardt-Goerg et al., 1993), the blocking of assimilate translocation, resulting from phloem injury, may trigger the senescence processes as suggested by the existing correlation between the timing of autumnal senescence and the amounts of starch (*Acer saccharum*; Schaberg et al., 2003).

An irregularly distributed adaxial stippling, especially along veins (Fig. 3F), frequently signals the induction of plant defenses following a mite infection. The thickness of the leaf blade is reduced following partial cell shrunking, cell walls are thickened and different phenolic compounds are accumulated in lumen and cell walls (not shown). Such reactions result from repeated piercing and incomplete sucking of the same tissue

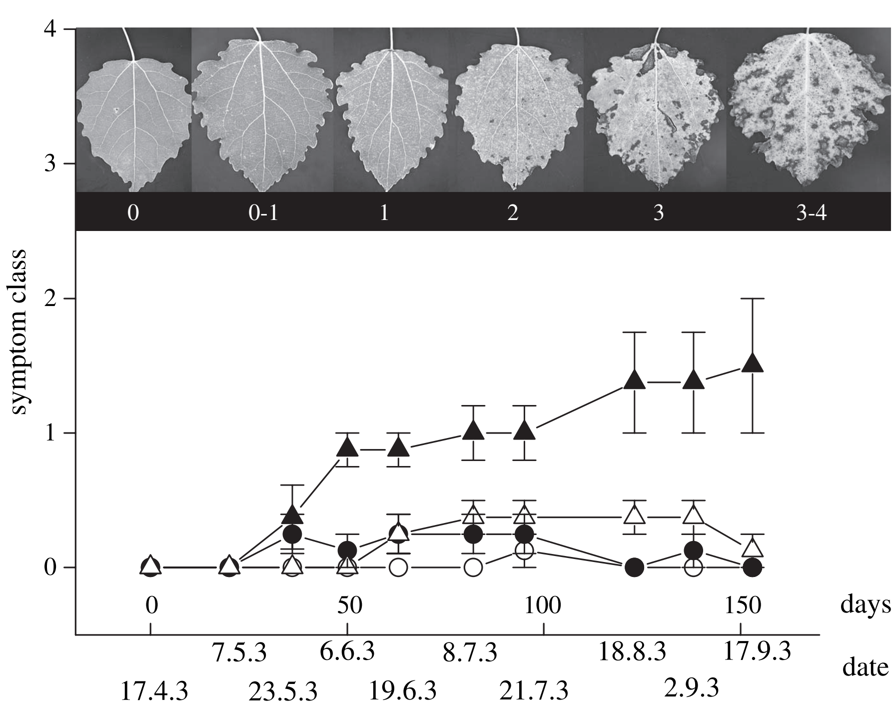

Fig. 4. Development of Zn symptoms in two provenances (open and closed symbols) of poplar (*Populus tremula* L.) following experimental exposure to heavy metal-contaminated (triangle) or uncontaminated (circle) acid forest soils in 3 m² lysimeter field plots (Birmensdorf, Switzerland). Mean values ± standard error, $N = 4$. Pictures: symptom gravity is ordered from 0–4 (0, asymptomatic; 1, adaxial and intercostal stippling; 2, necrotic spots appearing near the leaf basis; 3, intercostal necrotic patches; 4, > 1/3 of leaf necrotic).

portion by whole colonies directly established at the feeding site (detail in Fig. 3F). In contrast to moving small cicadas, mite activity thus results in lasting stress conditions. A parasitic colonization is generally involved when a biotic stress factor causes the induction of plant defenses to such a level that visible symptoms are produced. If confronted with a pathogen without any visible remnants, fruit bodies (Fig. 3G,H) or germinating spores and hyphae, even the identification of the class of stress factor (Fig. 1) requires laboratory analyses. Indications like brown rings of necrotic tissue (Fig. 3H), swollen instead of depressed necrotic dots (as in the case of abiotic stress) is frequently related to the effects of a growing mycelium. Dark dots and rings can result from programmed cell death processes, which, as a defense mechanism, originally evolved to limit the progression of pathogen infections (Heath, 2000; Rao et al., 2000).

3. Conclusion

Stress symptoms become visible in the foliage of trees and shrubs only once stress effects have largely changed the physiology and structure of the targeted tissues. Most visible symptoms discussed here thus correspond to terminal reactions and result from the necrosis or advanced degeneration of cells and tissues. Less acute but also well visible symptoms, like leaf reddening, are sometimes simultaneously recorded. As indicated here, such light-protective anthocyanins are inducible on different occasions and consequently have limited diagnostic potential. Other whole and even leaf discoloration symptoms closely resemble mineral element recycling during autumn and rarely provide a good diagnostic tool either. More attention to green hue changes could provide earlier detection of stress, however, this is more strenuous to implement.

Senescence patterns in tree crowns relate to—and for several aspects reveal—gradients in the crown and branch physiological activity. Acropetal and basipetal patterns during coloration development have a primarily inherited character, as they are highly species-specific. However, environmental constraints also play a still poorly understood role, as shown here in the case of the shading effects or discoloration traits in large crowns. More research on natural autumnal senescence is thus needed to better characterize the role of environmental factors (examining for example how senescence patterns vary in a given species along different ecological gradients). Catalogues of natural autumnal senescence symptoms should be established on a regional basis to provide background knowledge which is still missing in monitoring forest health.

Visible symptoms share interspecific traits which can be used to recognize the class of abiotic or biotic stress factors. Development features and distribution gradients are particularly useful to sort out otherwise similar injuries in the foliage. As already mentioned in the case of autumnal senescence, branch and crown gradients of symptoms caused by abiotic stress are also thought to mirror gradients in the leaf physiology. The effects of stress not only determine the morphology of the visible symptoms in foliage but also the direction of the branch gradient as shown here with the opposing directions between natural senescence and ozone stress gradients in beech. Accumulative stress is thus generally indicated by acropetal symptom gradients at branch level. Resemblance in visible symptom expression can result from similar effects of the stress factors. Adaxial stippling, for example, can appear with several sources of oxidative stress. Light intercepting compounds can be inlayed as a response to different stress sources, directly or indirectly damaging the chloroplastic machinery. Edge and tip necroses caused by many different stress factors appears to have some common—but still poorly understood—physiological origin linked to a disturbance in water and mineral nutrition. Each of the above type of visible symptom has a stress-specific indication value but to a still unknown degree. Evenly discolored foliage, however, appears to be a less specific symptom. It corresponds to an acceleration of foliage turnover as frequently found in many stresses. In the case of a biotic infection, the symptom display is mainly dependent on the specific interaction between the organisms involved but the class of infective parasite can often be recognized on the basis of the visible symptoms. The physiological and structural changes leading to different visible symptoms and gradients thus need further investigation in view of improving our diagnostic skills. In the presently changing climatic conditions, with expected shifts of the present vegetation zones, such an improvement would allow us to detect and monitor the effects of the evolving environmental constraints.

Acknowledgements

We thank Terry Menard for technical help while preparing the manuscript.

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