The relation between stand vitality and leaf miner density in beech and common oak

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Abstract: Collaborators of the Tinea foundation studied the density of leaf mines of beech and oak in The Netherlands in stands with different vitality. Random samples of 150 leaves were taken in late October, in the years 1992-1998. Only lepidopterous mines were studied; the *Phyllonorycter* mines and some *Stigmella* mines of oak were grouped. The stand vitality was expressed as a value ranging from 1 (healthy) to 4 (dead or moribund). Contrary to our expectation, the least healthy stands showed the lowest mine densities. Morever, the average mine density over all samples seems much higher than what perspires from the literature. We tentatively explain these observations by the assumption that stands with vitality 1 in fact are less healthy than was assumed; a strong nitrogen deposition is known to enhance the visual appearance of trees, but at the same time to damage the mycorrhiza system. Literature suggests that sap-sucking and ectophagous herbivores are more favoured by air pollution and heavily stressed plants than miners. In stands with a reduced vitality therefore direct and indirect competition, possibly also changes in the physical and chemical composition of the leaves, would reduce the miner densities.

A practical result of this study is that the number of leaves with at least one tentiform mine gives a good indication of the stand vitality in both tree species.

Keywords: air pollution; forest health; leaf miners; plant stress; The Netherlands

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Introduction

The condition of the forests in Western Europe is a matter of concern. Although the doom scenario of a large-scale 'Waldsterben' probably is an exaggeration (Ferretti, 1997), factors like dry and wet deposition of oxides of nitrogen and sulphur and of ammonia, elevated ozone levels, and climate change have contributed to a marked decline in the health of our forests (Heliovaara & Vaisanen, 1993; Kaus et al., 1996). The mechanism behind the declining vitality of trees is complex, and involves the complete forest ecosystem, including the chemical and physical condition of the soil and its mycorrhiza component (Kuyper et al., 1990). In The Netherlands, probably the main cause of damage is a high deposition of nitrogen compounds, exceeding critical levels on a wide scale (Breemen & Van Dijk, 1988). One of the results of this is a progressive acidification of the soil, leading, among other things, to high levels of mobile aluminium and manganese, which are potentially phytotoxic (Van der Eerden et al., 1998).

Also, the role that is played by insects in this phenomenon has many sides. Outbreaks of insects, including newly introduced species, have contributed locally to the decline in general condition of the trees (Moraal, 1997). On the other hand, high densities of phytophagous insects on forest trees are often an early warning that the stand is under stress by atmospheric pollution (Baltensweiler, 1985; Docherty et al., 1997; Riemer & Whittaker, 1989; Speight & Wainhouse, 1989). In many cases therefore the outbreak of insect pests is more of a symptom than of a cause. Because leaf miners are an inherent element of the insect load of forest trees, we are interested in the relation their abundance might have with the vitality of their host plants.

Much work is being done at present in Western Europe to monitor the condition of the forests. However, criteria for this purpose are not very well defined. Factors like the foliage mass or the discolouration of the foliage cannot be measured without subjective estimates (Ferretti, 1997).

There is a general prediction that in stressed plants both performance and population density of phytophagous insects will be enhanced, probably because stressed plants have a higher content of soluble nitrogen compounds and sugars, and a reduced concentration of defensive compounds (e.g. Bolsinger & Flückiger, 1987, 1989; De Bruyn, 1995; Feeney, 1968, 1970; Foggo et al., 1994; Riemer & Whittaker, 1989; White, 1984; papers in Heinrichs, 1988; see also Mattson, 1980). Phytophagous insects respond not only to natural stresses, like drought, but also to stress that is connected with man-induced air pollution (Alstad et al., 1982; Führer, 1985; Riemer & Whittaker, 1989). Most of the studies aimed at the effect of nitrogen deposition on phytophagous insects have found an increase in insect performance (Docherty et al., 1997). Also, it may be expected that the protection against phytophages that plants receive from endophytic fungi is eroded by air pollution (Saikkonen, 1994).

The prediction that insects perform better on plants under pollution stress, however attractive, seems not to be generally true, as ambiguous or opposite effects have been found in several experimental studies (e.g. Koricheva et al., 1998; Meyer & Root, 1996; Price, 1997; Speight et al., 1998; Speight & Wainhouse, 1989). Mopper & Whitham (1992) therefore proposed to distinguish between acute stress, such as caused by a drought period while the insect is feeding on the plant, and sustained stress, such as caused by chronically unfavourable soil conditions; their contention was that the plant-stress hypothesis would apply only in the second situation. Because the stress that is associated with the forest decline is of the chronic type (Koricheva, 1994), our initial hypothesis was that leaf miners would show a pattern of abundance that is inversely proportional to the health of the hostplant, at least at low or moderate levels of decline (cf. Martel & Maufette, 1997). In fact, we hoped that it would be possible to obtain an estimate of the tree vitality by counting the number of leaf mines (see also Lokke et al., 1996). In this paper we will report on the lepidopteran leaf mining fauna of the beech, *Fagus sylvatica* L., and the common oak, *Quercus robur* L. The data on which we base this report have been accumulated by a group of amateurs with a strong interest in faunistics of leaf mining insects, coordinated by the Tinea foundation.

Leaf miners

The larvae of a considerable fraction of smaller insects live inside parenchyma or epidermis tissues of plant leaves. This ancient (Labandeira et al., 1994) feeding behaviour results in characteristic feeding patterns visible on the leaves and known as leaf mines (Connor & Taverner, 1997; Hering, 1951; Hespenheide, 1991). The choice of leaf miners as monitoring organisms seems appropriate, for several reasons. Identification difficulties are limited to a large extent. Leaf miners are monophagous or oligophagous, implying that identification problems are limited to the restricted number of species occurring on the hostplant species. Moreover, mining behaviour, and therefore the shape of the mines, often varies strongly among the species, but is fairly constant within them (Hespenheide, 1991). The relation of the mining larva with the hostplant is very strong. Because it spends his whole life on one hostplant, the larva is maximally influenced by the physiological condition of this single plant individual (Waddell & Mousseau, 1996). Abiotic factors, in particular weather conditions are buffered inside the mine, and therefore will have less influence on miners than that on free-living larvae (Gaston et al., 1991), although temperature remains influential (Day & Watt, 1989; Idso et al., 1993). Leaf mines can be sampled much more easily and quantitatively than free-living organisms. Finally, even when a leaf miner leaves his mine or emerges, its trace remains in the leaf. In fact, many mining species are multivoltine, and by sampling at the end of the leaf season a grand total of the population of the miner can be estimated.

Table 1. List of the species that were monitored, with their taxononic position and host plant. (Tabel 1. Lijst van de soorten die werden geteld, met hun taxonomische plaats en waardplant.)

miner	family	host
Eriocrania subpurpurella (Haworth) ***	Eriocraniidae	*Quercus*
Ectoedemia albifasciella (Heinemann)	Nepticulidae	*Quercus*
E. heringi (Toll) ***	-"-	*Quercus*
E. subbimaculella (Haworth)	-"-	*Quercus*
Stigmella atricapitella (Haworth) **	-"-	*Quercus*
S. basiguttella (Heinemann)	-"-	*Quercus*
S. hemargyrella (Kollar)	-"-	*Fagus*
S. roborella (Johansson)	-"-	*Quercus*
S. ruficapitella (Haworth) **	-"-	*Quercus*
S. samiatella (Zeller) **	-"-	*Quercus*
S. svenssoni (Johansson) **	-"-	*Quercus*
S. tityrella Stainton	-"-	*Fagus*
Heliozela sericiella (Haworth) ***	Heliozelidae	*Quercus*
Tischeria dodonaea (Stainton)	Tischeriidae	*Quercus*
T. ekebladella (Bjerkander)	-"-	*Quercus*
Bucculatrix ulmella Zeller	Bucculatricidae	*Quercus*
Acrocercops brongniardella (Fabricius) ***	Gracillariidae	*Quercus*
Phyllonorycter harrisella (Linnaeus) *	-"-	*Quercus*
Ph. heegeriella (Zeller) *	-"-	*Quercus*
Ph. maestingella (Müller)	-"-	*Fagus*
Ph. messaniella (Zeller) *	-"-	*Quercus*
Ph. muelleriella (Zeller) *	-"-	*Quercus*
Ph. quercifoliella (Zeller) *	-"-	*Quercus*
Ph. roboris (Zeller) *	-"-	*Quercus*
Ph. saportella (Duponchel) *	-"-	*Quercus*

* Grouped as 'tentiform mines on oak'
** Grouped as 'other mines on oak'
*** Excluded from the calculations

Material and methods

As an aid for the identification of the mines a manual was compiled, where the mines were illustrated and keyed, and the sampling procedure was outlined (Ten Broeke et al., 1996). Table 1 lists the lepidopteran species that mine with some regularity on beech and oak in The Netherlands. Some lepidopteran species that were difficult to identify, and all non-lepidopteran mines were grouped as 'other mines'. Also, the mines made on oak by *Phyllonorycter* species are difficult to identify reliably, and are grouped therefore as tentiform mines. Four other species were left out of consideration, either because they occurred in low numbers *(Heliozela sericiella* (Haworth) and *Ectoedemia heringi* (Toll)) or because their mines are made early in the season, making counts in late autumn less reliable *(Eriocrania subpurpurella* (Haworth) and *Acrocercops brongniardella* (Fabricius)).

The field work was performed in the period 1992-1998. Samples were taken on plots, scattered over The Netherlands, once a year between October 15th and 31st. Per plot, ten (oak) or five (beech) trees were sampled. Each sample consisted of 150 leaves, taken at random, as far as the hand can reach when standing on the ground, at the best-illuminated side of the tree. Not all plots were sampled each year.

As part of a European project aimed at monitoring the vitality of the European forests, the vitality is measured at a large number of points in The Netherlands each year by the Ministry of Agriculture (Hilgen & Reuver, 1996). Basically, the health of 25 randomly selected individual trees in a plot is determined, based on discolouration of the leaves and the estimated loss of leaves. Each tree receives a score between 1: healthy and 4: (almost) dead. The vitality of the plot is taken as the average of the 25 observations. (Thus, the vitality index has the counter-intuitive meaning that the highest values signify moribund trees.) In most of the plots where mines were sampled forest vitality had been measured by the Informatie en Kenniscentrum Natuurbeheer, Ministry of Agriculture, Wageningen; in some plots this was done by the third author. Practical reasons prevented as a rule to take the leaf samples from the actual trees that had been used for the vitality estimate; nor was it always possible to sample the same trees in consecutive years. Per tree, the total number of mined leaves in the sample was counted, and for each miner species (or species group, viz. the tentiform mines on oak), both the total number of mines in a sample and the number of mined leaves.

For the statistical calculations, all counts were transformed as $x' = \log(x+1)$. This made the distribution reasonably normal. The average counts differed appreciably from year to year. We removed this effect by computing $x'' = x'$ minus the average of x' per species per year, and performing all tests on x''. In the text below we will use the term ‘crowding’ of a species to denote the average number of mines in those leaves that contain at least one mine (in other words, the number of mines observed, divided by the total number of mined leaves); crowding was calculated after the raw values.

Results

Clumped distributions

Under the (untested) assumption that the distribution of mines follows a Poisson distribution, it is possible to calculate the number of occupied leaves that can be expected, given the number of leaves sampled and the number of mines found. (As the number of leaves sampled we took 150 times the number of trees in which the species was found at least once; in other words, trees in which a species was not met were left out of consideration. This is the conservative approach). As table 2 shows, in all species in beech the expectation exceeds the observed numbers, in the more numerous species significantly. The distribution of the mines therefore clearly is clumped. Some species, like *Tischeria ekebladella* (Bjerkander) make large blotch mines, and it is physi-

Table 2. Number of trees, crowding, number of mines, and number of mined leaves for each species. In two following columns the number of leaves is given that could be expected when the mines would follow a Poisson distribution, and the probability of the observed difference (two-tailed χ^2-test). Tabel 2. Aantal bomen, de pakking, het aantal mijnen, en het aantal gemineerde bladeren voor elke soort. De kolom ‘exp’ geeft het aantal mijnen dat kan worden verwacht als de verdeling van de mijnen over de bladeren toevallig zou zijn (‘Poisson-verdeling’); de laatste kolom geeft de waarschijnlijkheid van de waargenomen afwijking (tweezijdige chi-kwadraat test.)

miner	trees	crowding	mines	leaves	exp.	*P*
P. maestingella	191	1.21	5257	4339	4803	0.0097
S. hemargyrella	105	1.05	367	348	363	0.3787
S. tityrella	161	1.14	1450	1269	1407	0.0548
other species (beech)	106	1.09	860	789	837	0.1970
all species (beech)	199	1.25	8228	6564	7191	0.0065
B. ulmella	235	1.44	2127	1477	2064	0.0003
E. albifasciella	243	1.31	1973	1507	1921	0.0021
E. subbimaculella	142	1.17	694	591	683	0.0609
S. basiguttella	153	1.07	512	478	506	0.2618
S. roborella	208	1.06	657	620	650	0.2770
T. ekebladella	174	1.09	571	524	565	0.1901
T.dodonaea	42	1.04	97	93	96	0.5645
tentiforms	336	1.40	11424	8169	10222	0.0000
other species (oak)	321	1.12	3531	3158	3405	0.0398
all species (oak)	347	1.51	21902	14462	17878	0.0000

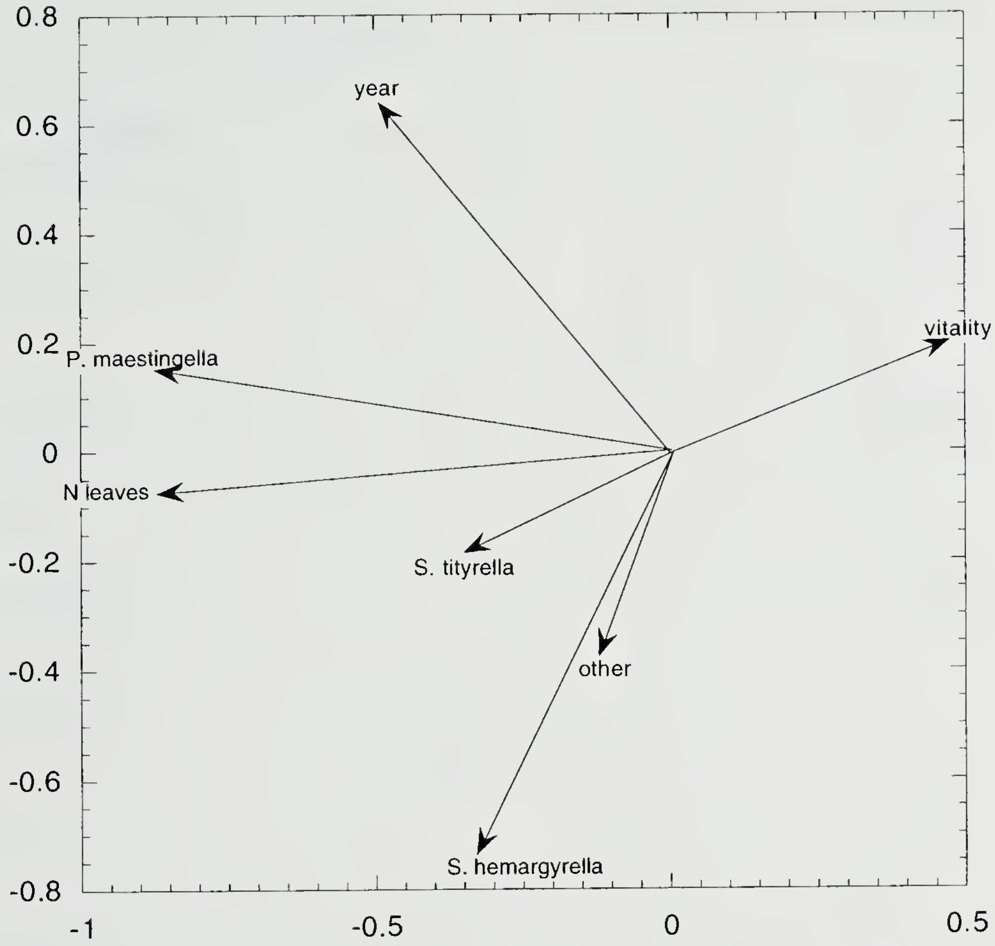

Fig. 1. Beech: ordination of year, vitality, total number of mined leaves, and number of mines per species (PCA). (Beuk: ordinatie van jaar, vitaliteit, het totaal aantal gemineerde bladeren, en de aantallen mijnen van de verschillende soorten.)

cally impossible for these mines to be as strongly clumped as the tiny mines of *Bucculatrix ulmella* Zeller. Clumping is also significant when all species are pooled ('all species'), which means that also mines of different species are more often found in the same leaf than a random distribution would imply.

Beech

Out of a sample of 150, between 1 and 121 leaves had at least one mine (average 33.0); the number of mines per sample ran from 1 to 237 (average 42.1). The crowding on average amounts to 1.2. The number of mines of *Stigmella tityrella* Stainton and *S. hemargyrella* (Kollar) in a sample vary between 0, and 66 and 25, respectively, but *Phyllonorycter maestingella* (Müller) mines may be much more numerous, with up to 221 mines (average 28.6 mines, or 22.4 leaves). Fig. 1 shows a factor plot of the vitality, year, and the number of mines of the different species, and the total number of mined leaves. The plot predicts that there will be little correlation between vitality and year, and that there will be a more or less clear negative relation between the mine data and the vitality.

Table 3 gives a summary of the regression

Table 3. Beech: regressions of the transformed number of mined leaves and number of mines, and of the crowding, on the stand vitality. Results are shown only when $P \leq 0.05$. (Tabel 3. Beuk: regressie van het getransformeerde aantallen gemineerde bladeren en mijnen, en van de pakking, op de perceel-vitaliteit. Resultaten worden alleen getoond als $P \leq 0.05$).

	mined leaves				mines				crowding			
	df	*b*	*P*	R^2	df	*b*	*P*	R^2	df	*b*	*P*	R^2
all species	192	-0.3789	≤0.0001	12.2	237	-0.1440	0.0013	3.9	192	-0.1649	0.0003	6.2
P. maestingella	187	-0.4279	≤0.0001	13.8	237	-0.1714	0.0017	3.7	183	-0.1628	≤0.0001	7.6
S. hemargyrella	187	-	-	-	237	-0.1404	0.0080	2.5	102	-	-	-
S. tityrella	187	-	-	-	237	-	-	-	154	-	-	

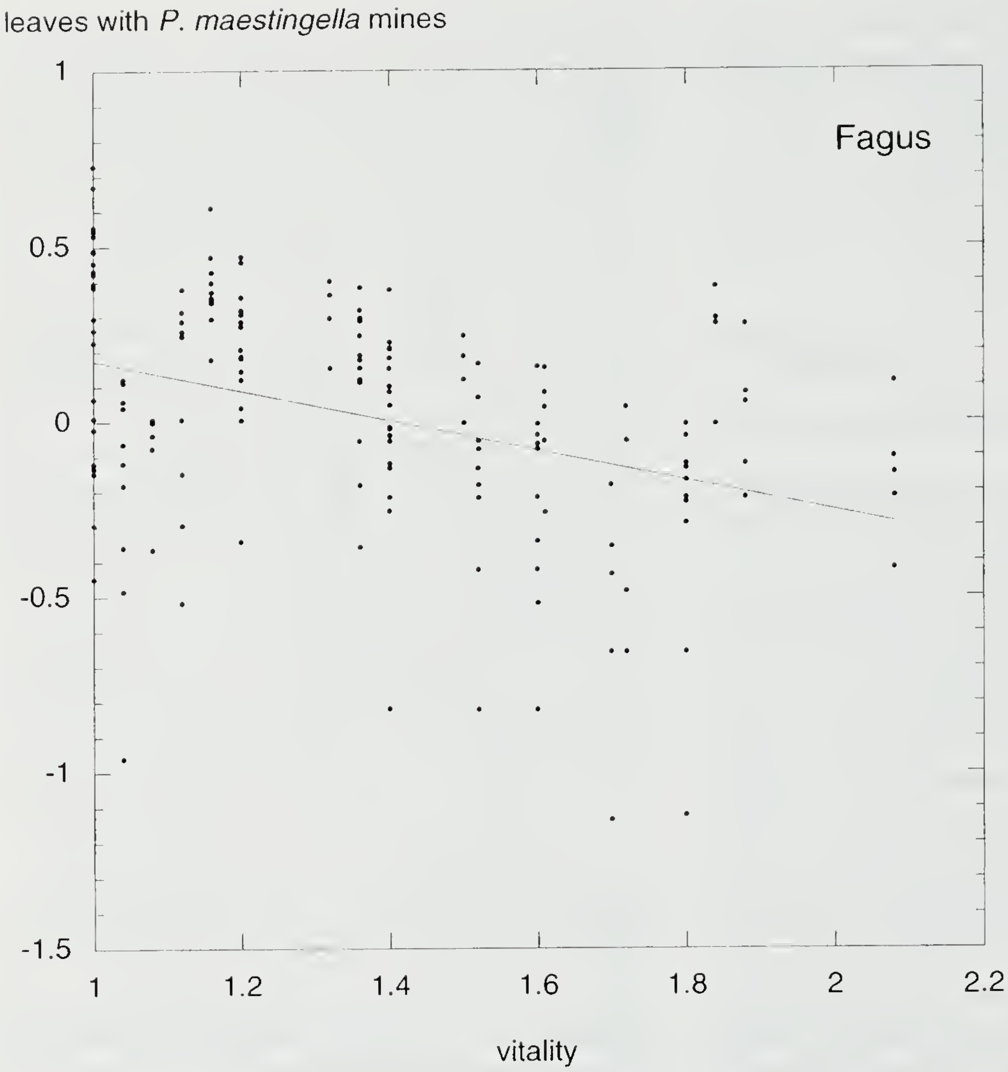

Fig. 2. Beech: regression of the transformed number of leaves mined by *P. maestingella* on the stand vitality.

of the main data columns on the vitality. For all species combined this regression is significant for the (transformed) number of mined leaves and number of mines, and for the crowding. Like it was found in other tests, there is an appreciable difference in the statistical behaviour of mines and mined leaves. Because the mining fauna is dominated by *P. maestingella* (cf. table 1), not surprisingly the same results apply to that species alone. In all cases the regression is negative, implying that trees with the lowest vitality index, i.e., the most healthy ones, have the highest number of mined leaves, contrary to our initial expectation. Fig. 2 shows the regression for the transformed number of mines leaves of *Ph. maestingella*.

Oak

The number of mined leaves fluctuated be-

Table 4. Oak: regressions of the transformed number of mined leaves and number of mines, and of the crowding, on the stand vitality. Results are shown only when $P \leq 0.05$. (Tabel 4. Eik: regressie van het getransformeerde aantallen gemineerde bladeren en mijnen, en van de pakking, op de perceel-vitaliteit. Resultaten worden alleen getoond als $P \leq 0.05$).

	mined leaves				mines				crowding			
	df	*b*	*P*	R^2	df	*b*	*P*	R^2	df	*b*	*P*	R^2
all species	326	-0.4928	≤ 0.0001	4.5	433	-0.6569	≤0.0001	6.3	276	-0.4009	≤0.0001	6.8
B. ulmella	317	-0.2462	0.0008	3.2	383	-0.3011	0.0001	4.6	216	-	-	-
E. subbimaculella	317	-	-	-	383	-	-	-	130	-0.4141	0.0022	3.2
S. basiguttella	317	-	-	-	383	-0.3003	0.0092	1.5	142	-	-	-
T. dodoneae	317	-	-	-	327	-	-	-	40	-	-	-
T. ekebladella	317	0.2150	0.0269	1.2	383	0.2905	0.0036	1.9	158	-	-	-
tentiform mines*	317	-0.6462	≤0.0001	20.2	433	-0.6583	≤0.0001	11.3	275	-0.4306	0.0001	4.9
other species	317	-	-	-	383	-	-	-	300	-	-	-

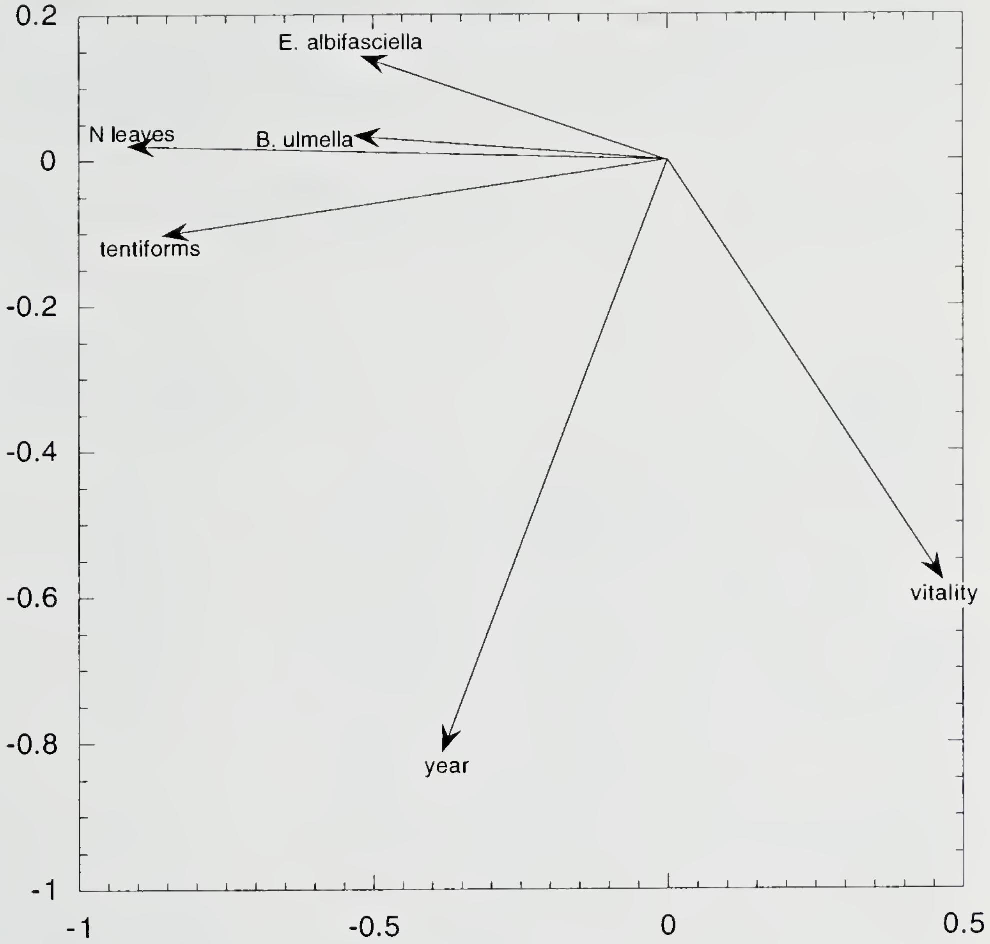

Fig. 3. Oak: ordination of year, vitality, total number of mined leaves, and number of mines per species (PCA). (Eik: ordinatie van jaar, vitaliteit, het totaal aantal gemineerde bladeren, en de aantallen mijnen van de verschillende soorten.)

tween 3 and 130 per sample (mean 41.7). The average number of mines per 150 leaves was 62.3 (33.2 for the complex of the tentiform mines). The crowding ran from 0.8 – 4.3 (mean 1.4).

Fig. 3 gives a factor plot of the main data columns (only the most numerous species are included). The plot suggests that year, vitality, and the miner densities vary more or less independently.

The vitality ranged from 1.0 to 3.8. Table 4 gives the regression of the main data groups on the vitality. It is clear that, like in beech, there is an overall negative relation between the most numerous miners, viz. the tentiform group, on the vitality, both at the level of number of mines, mined leaves, and crowding; again, the most significant relation is with the number of mined leaves. Also, both the total number of mines and of mined leaves responds negatively to the vitality index. The other species of miners show a less clear pattern. Fig. 4 presents the regression of the transformed number of leaves with tentiform mines on the stand vitality.

Discussion

The distribution of leafminers in the canopy is known not to be uniform, and our method of sampling should therefore be taken into consideration. In particular, Overgaard Nielsen & Ejlersen (1978) reported that in Denmark *Phyllonorycter maestingella* and *Stigmella hemargyrella* mainly attack the understory of beech trees; Phillipson & Thompson (1983, working in Oxford) confirm this for *P. maestingella*, but not for *Stigmella* spp. Jordan (1995) found in Germany the majority of *Tischeria ekebladella* in the lower reaches of the crown of *Quercus robur*. Miller (1973) mentions an increasing density of *Phyllonorycter* mines from the top of oak trees to the low regions of the crown. Also, the sampling instruction that leaves should be taken from the sunny side of the crown is of relevance, since Overgaard Nielsen & Ejlersen (l.c.) found that beech miners preferably attack shaded leaves.

Feeding by chewing insects may interfere with population development of mining or which would imply little direct competition. Bultman & Faeth (l.c.) on the other hand found the seemingly paradoxical result that the coexistence of two different species in the same leaf resulted in higher than average survival, while the opposite was true for single occupants, or two conspecific ones. They explain this by assuming that oak leaves differ in quality, and that females select superior leaves regardless of the presence of other miners. The higher mortality where conspecifics co-occur in the same leaf was attributed to their combined higher appearance to predators and parasitoids, which implies competition through indirect interference. A limiting role of high-quality oviposition sites has also been found in other leaf-miners (Quiring & McNeil, 1987 and references given there). Also Denno et al. (1995) warn not to easily explain aggregation as an indication of the absence of substantial intraspecific interaction. Faeth & Simberloff (1981), working with a gracillariid on an American oak species, artificially increased the density of the leaf-miner in the absence of most of its parasites and predators by enclosing an experimental tree in a cage of fine-meshed screening. This brought the (total) mine densities up from ≤ 25 to as much as 140 per 1000 leaves. This manipulation strongly increased, rather than decreased, larval survivorship. Here too the authors conclude that intraspecific competition at normal densities plays no role of any significance. These findings fit well in the general notion that parasitoids and predators keep population densities of phytophagous insects in nature generally at levels too low for significant inter- or intraspecific competition to occur (Hairston et al., 1960; Rathcke, 1976; Speight et al., 1998).

The density of mines in our samples seems to be relatively high: beech: all mines 281, *Phyllonorycter maestingella* alone 191; oak: 424, tentiforms alone 215 (all values in this paragraph are mines per thousand leaves). Miller (1973) mentions values for *P. maestingella* of 54 and of 40 and 48 for the combined densities of the two *Phyllonorycter* species on oak. The values mentioned by Bultman & Faeth (1985a) range, for individual Lepidoptera species, from 0.04 to 20, very much lower values still. Faeth (1980) writes that in eastern North America leafminers on oak usually remain at much lower values than 10%. Jordan (1995) mentions an average density of *Tischeria ekebladella* of less than 1% (2% in our case). Only Connor & Beck (1993), working with *Cameraria hamadryella* (Clemens) on *Quercus alba* L., found higher values, viz. a staggering 22790, but only in outbreak situations; the endemic value being only 4. Mopper et al. (1984) found on average of 270 and 30 mines of *Stilbosis quadricustatella* (Chamberlain) on two American oak species. These comparisons must be taken with caution, because it is not always clear whether all mines are counted or only occupied ones. Moreover, the size of the mines differs strongly from one miner species to the other.

Our results show that the relation between vitality of the stand and the number of leafmines does not follow the positive relation that we anticipated. This agrees with the results of Martel & Maufette (1997), who found a weak indication of enhanced performance of exposed-feeding caterpillars on trees stressed by air pollution, but a distinct decline in mining Lepidoptera larvae. This may simply be another example of the ‘plant stress paradox’, the frequently observed phenomenon that herbivorous insect populations do not follow the prediction that they should benefit from plant stress, but rather decline; many examples of this can be found in Mopper & Whitham (1992). Yet, the relatively high average mine densities observed by us suggest an alternative explanation. There are reasons to believe that in The Netherlands even trees that look perfectly normal and healthy actually are stressed. In particular, there is an alarming decline in plant diversity of the forest undergrowth (summarized in Van Eerden et al., 1998) and of ectomycorrhizal fungi, even in seemingly intact forest ecosystems (Ozinga & Baar, 1997). The high mine density may be another early warning. Van Eerden et al. (l.c.) warn that vitality, as measured by crown appearance, may be a misleading indicator; in fact, excessive nitrogen deposition may lead to a situation where vigorous growth and increased stress sensitivity go hand in hand (cf also Kuyper et al., 1990). Perhaps the somewhat emotional, subjective notion of tree vitality is less useful than we thought.

As a way out of the plant stress paradox, Mopper & Whitham (1992) proposed the 'stress as a continuum' hypothesis, which says that insects perform best at intermediate levels of plant stress. This ties in with the general impression that severe air pollution or plant stress is detrimental to the herbivore fauna, while moderate or low pollution / stress levels favour phytophagous insects (Ball & McLeod, 1997; Hughes, 1988). Applying this hypothesis to our data, this means that trees in stands with a vitality of about 1 are already so stressed as to support a higher-than-usual herbivore fauna, while the conditions in stands with higher vitality indices are suboptimal. This may be because of the physiological condition of the trees by itself. It is not unlikely, however, that this factor is complicated, even brought into a positive feedback loop, by herbivory, possibly by sap-sucking or chewing insects, that themselves are often favoured by the high plant stress (Bolsinger & Flückiger, 1987, 1989; Heliovaara & Vaisanen, 1993; Martel & Mauffette, 1997). West (1985) demonstrated that damage caused to leaves by chewing insects, and also experimental mechanical damage significantly reduced the survivorship of leaf-mining insects. He even found evidence that the phenology of *Phyllonorycter* species that mine very late in the season, when nutritional quality of the leaves is minimal is an escape mechanism to avoid the period that most chewing caterpillars are active. Also Faeth (1985) found that females of the leaf-mining cosmopterygid *Stilbosis juvantis* (Hodges) oviposit preferably on undamaged leaves. Yet, like chewing insects, also leaf miners induce chemical changes in the leaves they inhabit (Karban & Myers, 1989, Ohgushi, 1992). Birch leaves mined by *Eriocrania* spp. have higher phenolic contents and precipitate proteins faster than unmined leaves, and are significantly avoided by *Coleophora serratella* (Linnaeus) (Lawton, 1986; Valladares & Hartley, 1994), just like leaves that were mechanically damaged (Bergelson et al., 1986; Haukioja, 1990; Haukioja & Niemelä, 1977). The same explanation may be invoked for the negative correlation between the number of *Eriocrania* mines and that of *Epirrita autumnata* (Borkhausen) larvae on the same birch branch (Bylund & Tenow, 1994). Perhaps the multitude of biological interactions like these may explain why Koricheva et al. (1998) find at the same time little general support for the plant stress hypothesis and a great variation in direction and magnitude of the insect response.

More proximate mechanisms may exist as well. Stressed trees have a reduced canopy density, exposing the leaves to stronger insolation; this affects both the temperature and the physical conditions of the leaves, two factors for which miners are quite sensitive (Bultman & Faeth, 1988; Martel & Maufette, 1997). The leaves of trees under stress tend to be relatively small, which may negatively influence miner life expectancy (Bultman & Faeth, 1985b, 1988). An enhanced performance of sap-sucking insects will result in more sooty mould, which may interfere with oviposition behaviour.

It should be borne in mind that all we could do was to correlate our data with an estimate of vitality that is the average of 25 trees, that in most cases are not included in the sample. Yet, within a stand, there is strong variability in tree condition, and in plant chemistry (e.g., Bergelson et al., 1986). This probably explains the strong within-stand variation in mine density that is illustrated in fig. 2 and 4, as was also found by Mopper & Simberloff (1995). A logical extension of our work therefore would be to connect mine densities with vitality data of individual trees.

Yet, crude as they are, our results show that mines seem ideally suited for monitoring stand conditions. Even identification difficulties are absent, since, at least in oak and beech, the least technically demanding measure, the number of leaves with at least one tentiform mine, gives the best results.

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Samenvatting.

Het verband tussen bosvitaliteit en de bladmineerderbezetting bij beuk en zomereik. Medewerkers van de stichting Tinea hebben in de jaren 1992-1998 bladmonsters onderzocht van beuk en eik die groeiden in percelen met uiteenlopende vitaliteit. De monsters bestonden uit 150 bladeren die eind oktober aselect werden verzameld. De vitaliteit van het perceel werd uitgedrukt in een index die loopt van 1 (gezond) tot 4 (stervend of vrijwel dood). Alleen vlindermijnen werden geteld; de *Phyllonorycter*-mijnen en enkele lastige *Stigmella*-mijnen van eik werden als één groep behandeld (tabel 1). Aan de hand van de waarnemingen berekenden wij de 'pakking' (het aantal mijnen van een soort, gedeeld door het aantal door die soort gemineerde bladeren). Voor statistische bewerkingen van aantalsgegevens is het gebruikelijk de waargenomen getallen (x) te vervangen door $x' = \log(x + 1)$. Omdat de gemiddelde aantallen mijnen van jaar tot jaar sterk uiteenliepen, werd terwille van de vergelijkbaarheid nog een tweede transformatie toegepast: $x'' = x'$ min het gemiddelde van x' voor de betreffende soort en voor het betreffende jaar. Deze gecorrigeerde waarde werd berekend voor het aantal mijnen, en het aantal gemineerde bladeren, voor alle redelijk talrijke soorten.

Een vergelijking van het aantal waargenomen gemineerde bladeren met de aantallen die zouden mogen worden verwacht wanneer de mijnen toevalsmatig over de bladeren zouden zijn verdeeld laat zien dat er zowel binnen één soort, als binnen alle soorten tesamen, sprake is van een duidelijke clustering (tabel 2): mijnen, van dezelfde of van verschillende soorten, komen meer dan toevallig voor op eenzelfde blad. Kennelijk verschillen bladeren onderling in aantrekkelijkheid.

Hoewel het onze verwachting was dat de grootste aantallen mijnen op zouden treden in de ongezondste percelen, bleek het omgekeerde het geval te zijn (fig. 1 en 3, tab. 3 en 4). Het duidelijkste (negatieve) verband tussen de waarden van x'' en de vitaliteit was te zien bij het aantal gemineerde bladeren, enerzijds door de vouwmijn van de beuk *(P. maestingella)*, anderzijds door het gezamelijke complex van vouwmijnsoorten van de eik (fig. 2 en 4). Ook het aantal mijnen en de pakking vertonen dit negatieve verband, zij het minder uitgesproken. Een vergelijking met de literatuur lijkt erop te duiden dat het aantal mijnen in onze monsters ongewoon groot is. Deze twee elementen samen zouden erop kunnen wijzen dat percelen met vitaliteitsklasse 1 in feite minder gezond zijn dan tot dusver wordt aangenomen. Dat is niet onwaarschijnlijk: een sterke stikstofbelasting als gevolg van luchtverontreiniging kan maken dat bomen een vitale indruk maken maar in feite een verzwakt mycorrhiza-systeem hebben. In de literatuur zijn aanwijzingen te vinden dat luchtverontreiniging, en gestresste planten, een aantal herbivoren-groepen bevoordelen, maar dit lijkt niet op te gaan voor mineerders. In percelen met een verminderde vitaliteit zouden daarom rechtstreekse en indirecte competitie met andere herbivoren-groepen, en mogelijk ook veranderingen in de fysisch-chemische eigenschappen van de bladeren, tot lagere dichtheden kunnen leiden van bladmineerders.

Een praktisch resultaat van het onderzoek is dat het aantal bladeren met tenminste één vouwmijn bij zowel eik als beuk een bruikbare indicatie lijkt te geven van de gezondheid van het perceel.

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