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Pine mistletoe (*Viscum album* ssp. *austriacum*) contributes to Scots pine (*Pinus sylvestris*) mortality in the Rhone valley of Switzerland

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Summary

In recent years unusual high mortality of Scots pine (*Pinus sylvestris*) has been observed in the Swiss Rhone Valley. The exact causes, however, are not known. At a 2-ha monitoring plot, tree mortality and crown condition have been monitored since 1996. Between 1996 and 2004, 59% of the Scots pines died, most of them following the drought periods 1996–1998 and 2003–2004, while only 15% of the deciduous trees died. Crown transparency, needle discolouration, dead branch percentage, mistletoe (*Viscum album* ssp. *austriacum*) rating, *Tomicus* sp. shoot feeding, male flowering effect, tree stem diameter, crown shading and social tree class assessed in 1998 were used in a logistic regression model to predict tree mortality. Crown transparency, mistletoe rating and percentage of dead branches were found significant in the model and the probability of tree mortality increased with increasing rankings of these parameters. Needle discolouration could be used to substitute 'dead branch percentage' as predictor. While crown transparency increased with mistletoe rating, for trees in the same transparency class, trees with medium and heavy mistletoe infection were two to four times more likely to die than trees with no or only low mistletoe infection. For the surviving trees we found that trees with mistletoes showed a significantly higher increase in transparency in the year following a drought than trees without, while in a drought year the opposite was true. At the beginning of the observations no significant differences in transparency had been found between the trees with and without mistletoe. However, by the end of the observation period trees with mistletoe had significantly higher crown transparency. We conclude that mistletoe infection can be considered as both a predisposing factor for tree death, by increasing needle loss following drought and a contributing factor by increasing water stress during drought.

1 Introduction

In recent years unusual high tree mortality of Scots pine (*Pinus sylvestris* L.) has been observed in the Rhone valley of the Swiss Canton Valais (RIGLING and CHERUBINI 1999; RIGLING et al. 2004; DOBBERTIN et al. 2005b) and other inner-alpine valleys (CECH and PERNY 1998; VERTUI and TAGLIAFERRO 1998). The exact causes of the pine decline have not been established yet and are currently under investigation.

In the Valais Scots pine forests constitute 11% of the total forest area and range from the valley floor between 400 and 700 m a.s.l. to the sub-alpine forests at 2000 m a.s.l. Episodes of Scots pine decline in Valais have been reported throughout the 20th century and have often been attributed to fluoride emissions from aluminium factories (FLÜHLER et al. 1981; KIENAST et al. 1981). Following the installation of filter systems fluoride emissions decreased (RICKLI et al. 1989) and no further tree decline was reported in the vicinity of the factories. Since the 1990s a new pine dieback episode has been observed (RIGLING and CHERUBINI 1999; REBETEZ and DOBBERTIN 2004; RIGLING et al. 2004; DOBBERTIN et al. 2005b). On dying trees *Tomicus piniperda* L., *T. minor* Htg., *Ips accuminatus* Gyll., the buprestidae *Phaenops cyanea*

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F. (Dobbertin 1999; Rigling et al. 1999) and various blue stain fungi (*Ophiostoma* spp., *Leptographium* spp.; Carron 2000) were identified. Pine wood nematodes may also be involved in the decline process (Braasch et al. 2004; Polomski et al. 2006).

In almost all reports on pine decline in the inner-alpine valleys drought is mentioned as an inciting factor (Cech and Perny 1998; Vertui and Tagliaferro 1998; Rigling and Cherubini 1999; Bigler et al. 2006). However, Scots pine is known to be very drought-resistant and other more drought-susceptible trees were not affected (Rigling and Cherubini 1999). In Valais, annual mortality rates varied substantially between years and were highest following the drought years 1998 and 2003 (Dobbertin et al. 2005b). Mortality related best to drought stress of the prior summer (May–August) calculated as the difference between precipitation and calculated potential evapotranspiration. Mortality rates of pines, but not of other species, were higher at altitudes below 1100 m a.s.l. On plots exposed to drought stress mortality was significantly higher for Scots pine, but not for other tree species (Dobbertin et al. 2005b). Bigler et al. (2006) modelled mortality risk from tree ring width of dead and alive pines in Valais. They found that pine mortality risk increased following multiple years of drought.

Some authors considered the pine mistletoe (*Viscum album* ssp. *austriacum*) as a predisposing stress factor for pine mortality (Rigling and Cherubini 1999). Scots pine trees in Valais are frequently infested with pine mistletoe that extended their upward distribution during the last century (Dobbertin et al. 2005a). Pine mistletoe occurs almost exclusively on pine species (Barney et al. 1998). Pine mistletoe is able to photosynthesize but needs to take water and nutrients from its host tree. It is a xylem-tapping mistletoe (Calder and Bernhardt 1983).

Mistletoe infestation is correlated with higher crown transparency (Dobbertin 1999), which has been found in several studies to correlate with subsequent tree mortality (Neumann and Stemberger 1990; Schmid-Haas 1993). Higher tree mortality and transparency values also depend on the social status of the trees (Dobbertin and Brang 2001; Dobbertin 2005).

The objectives of this study were to test whether: (i) crown and tree condition variables, such as mistletoe infestation, crown transparency, dead branches, needle discolouration, social tree position or crown shading could be used to predict subsequent tree mortality; (ii) mistletoe infestation correlates with the increase in crown transparency and thus contributes indirectly or directly to the Scots pine mortality in the Swiss Rhone valley and (iii) trees infested with mistletoe reacted with increased needle loss to drought stress. One long-term monitoring plot in Valais, which has recently suffered from high pine mortality, was used to test these hypotheses.

2 Materials and methods

2.1 Data

The study site Visp is one of the Swiss long-term forest ecosystem research plots (LWF), which are part of the level II network of ICP Forests (International Cooperative Programme for the Monitoring of Long-range Transboundary Air Pollution Effects on Forests, de Vries et al. 2003). The 2.0-ha plot is located on a steep north-facing slope close to the valley floor at around 700 m a.s.l (latitude: +46°17′53″, longitude: +07°51′34″). The uneven-aged forest (30–70 years in age) is composed of roughly 80% Scots pines and 20% broadleaves [mainly *Sorbus aria* (L.) Crantz and *Quercus pubescens* Willd.]. The mean annual precipitation for the comparison period 1961–1990 at the near-by Meteoswiss climate station Visp was 600 mm and the mean annual temperature was 8.6°C. Years with <500 mm precipitation can be considered as drought years.

Since 1996 around 400 pines with a d.b.h. of at least 12 cm have been monitored. In March 1996, all standing trees with the minimum diameter were numbered. The status (alive or dead) of the trees was recorded. In July 1998, all trees were assessed for crown condition and each following summer all new dead trees were recorded. On a 0.5-ha subplot the crown condition of all trees was assessed annually in July.

The crown condition assessment included crown transparency, causes for transparency, foliage colour, dead branch and dead twig percentage, mistletoe occurrence, crown shading and social position. Crown transparency was assessed in comparison with a fully foliated reference tree using standard photographs (MÜLLER and STIERLIN 1990). Here, 0% transparency means fully foliated and 100% dead. Crown transparency, dead branches and dead twigs were assessed in 5% classes from 0% to 100%. Dead branches and twigs below the live crown and in the inner shaded part of the crown were not considered. Foliage colour was estimated for shaded leaves using the Munsell colour chart for plants (INNES et al. 1996). In this study foliage colour was converted to a binary variable (0 = no discolouration, 1 = discolouration). Trees with either at least 10% yellow needles (Munsell hue colour code ≤ 25) or the majority of needles in the yellow-green class (Munsell hue colour code = 32) were considered as discoloured. Up to two causes for crown transparency were noted. A cause was only recorded if – according to the judgement of the observer – it led to at least 5% additional transparency. The possible causes were insects (no defoliating insect occurred at the site, the only observed insect cause was shoot boring by *Tomicus* sp.), fungi (only on leaves/needles or branches), climatic factors (wind-broken branches or attrition), male flowering and human-caused damage. No or very few trees were assessed with fungi, climatic damage or human-induced causes. Therefore, only *Tomicus* shoot feeding and male flowering were used in the analysis. Crown shading was assessed in 10% classes, where 0% corresponds to a free-standing tree, and 100% to a tree surrounded and over-toped by neighbours. Due to the shade intolerance of Scots pine very few trees were found with a high degree of shading. Therefore, classes were combined as follows: 0–10% = no shading, 20–30% = low degree of shading, 40–50% medium degree of shading, ≥60% high degree of shading. Social tree position was recorded in five classes (predominant, dominant, codominant, intermediate and suppressed, KRAFT 1884). Mistletoe occurrence was recorded in four classes: 0 = no mistletoe, 1 = low mistletoe infestation with at least one mistletoe, 2 = medium mistletoe infestation with several large mistletoe bushes or many small plants found in the crown, 3 = heavy mistletoe infestation with many large mistletoes on at least one-third or more of the branches in the tree crown. The proportion of trees within these classes and the observed mortality rates since 1998 are presented in Table 1.

For the analysis of tree mortality we used the data of the crown condition assessment of the whole plot assessed before the onset of mortality in 1998. We tested which crown and tree parameters are associated with subsequent tree mortality until the summer of 2003. Annual assessments of crown transparency on the subplot were used to test for differences in transparency development between trees with and without mistletoes.

2.2. Data analysis

We first applied a categorical analysis of variance (SAS procedure – CATMOD, SAS INSTITUTE INC. 1989) to identify the significant variables for tree mortality. We applied a log-odds ratio ANOVA (GOTTSCHALK et al. 1998) to the main effects of the independent variables treating transparency, d.b.h. and percentage of reported dead branches and twigs as continuous variables and mistletoe occurrences, social tree position, crown shading and the causes for transparency (such as *Tomicus* shoot feeding, male flowering and climatic damage) as nominal variables. Significant main effects ($p < 0.05$) were retained and used in a logistic regression model.

Table 1. **Proportion of trees (total N = 379) and mortality rates since 1998 by assessed variable category in 1998**

Variable	Class	N (%)	Mortality (%)
d.b.h. (cm)	12–14.9	39.6	32.7
	15–17.9	23.7	30.0
	18–20.9	14.8	48.2
	21–23.9	10.3	48.7
	≥24	11.6	56.8
Social class	Predominant	0.8	33.3
	Dominant	16.4	45.2
	Codominant	75.7	36.9
	Intermediate	6.6	44.0
	Suppressed	0.5	50.0
Crown shading (%)	0–10	23.0	44.8
	20–30	39.1	39.9
	40–50	27.7	32.4
	≥60	10.3	38.5
Discoloured	No	82.1	32.8
	Yes	17.9	66.2
Transparency (%)	0–15	34.8	18.9
	20–30	39.8	33.8
	≥35	25.3	74.0
Dead twigs (%)	0	67.3	26.7
	5	22.2	57.1
	10	7.1	70.4
	≥15	3.4	92.3
Mistletoe rating	No	33.5	22.8
	Low	49.3	33.7
	Medium	13.5	82.4
	High	3.7	92.9
Tomicus shoot feeding	No	80.2	37.8
	Yes	19.8	42.7
Male flowering	No	83.9	36.5
	Yes	16.1	50.8

In order to test the applicability of the variables to predict tree mortality, a logistic regression model – the most commonly used model to predict the probability of a tree to die – was fitted (MONSERUD 1976). The logistic regression model had the following form:

$$\log[p/(1-p)] = a + \sum b_i \times x_i,$$

where $p = \Pr(Y = 1/x)$ is the probability of a tree to die and 'Y' is the binary response variable ($Y = 1$, if the tree has died and $Y = 0$ otherwise), 'a' is the intercept parameter, 'b_i' are the slope parameters and 'x_i' the explanatory variables. The LOGISTIC procedure in SAS software was used to fit the model (SAS INSTITUTE INC. 1989). As a maximum likelihood estimate the −2 log-likelihood was computed using the iteratively reweighted least-squares algorithm (SAS INSTITUTE INC. 1989). The likelihood ratio chi-square test statistics for the joint significance of the explanatory variables (HOSMER and LEMESHOW 1989) and the Akaike information criterion (SAS INSTITUTE INC. 1989) were computed and together with NAGELKERKE's (1991) generalized R^2 coefficient of determination used to compare models. Wald chi-square statistics were used for the parameter estimates. In the logistic model all variables were treated as continuous or ordered.

To test how mistletoe infection may affect needle retention we grouped the trees on the subplot that had survived the period of consideration and had been assessed annually in two classes of mistletoe occurrence. We computed the average mistletoe score for the period and classified the trees with a score ≥0.5 as mistletoe trees and the ones with <0.5 as mistletoe-free. We tested if the crown transparency of the two groups was significantly different at the beginning and at the end of the period, or if the change in transparency was different in any of the years using Kruskal–Wallis test statistics.

3 Results

In the crown condition assessment of 1998 roughly one-third of the pines had low crown transparency (0–15%) and every fourth tree had high transparency scores (≥35%, Table 1). Diameter distribution was skewed to the low diameters and three quarters of the trees were classified as codominant. Two-thirds of the trees were infected by mistletoes, and almost 20% with medium to high mistletoe rating. Between 15% and 20% of the trees had either discolouration, *Tomicus* shoot feeding or male flowering effects and every third tree had more than 5% dead branches or twigs (Table 1).

Of the 411 pines alive in 1996, 179 (44%) had died by 2002 and 241 pines (59%) by 2004 (Table 2). Of the 379 alive pines assessed for crown condition in 1998, 148 (39%) had died by 2003 (Table 2). Of the 74 pines alive in 1996 on the subplots, 43 (58%) had died by July 2004 (Table 2). In comparison, of the 40 deciduous trees alive in 1996 on the subplot only six (15%) have died since. Mortality was highest between July 1998 and July 1999 and between July 2003 and July 2004 (Table 2). The years with highest mortality rates followed the drought periods 1997/1998 and 2002/2004.

The categorical logistic regression using all variables found transparency, percentage of dead branches and twigs and mistletoe infection rating to be significant (Table 3). None of the tree competition/tree size variables (social position, crown shading and d.b.h.) was significant, neither were the observed causes of transparency (*Tomicus* shoot feeding and male flowering) nor discolouration. However, occurrence of dead branches and discolouration were confounded. When the variable dead branches was excluded discolouration became significant (not shown). The logistic regression using only the significant variables indicates increasing mortality probability with increasing scores of transparency, mistletoe infection and dead branches (Nagelkerke's $R^2 = 0.41$, Table 4). Using the estimated mortality probability that predicted the closest actual number of dead trees as a threshold, we classified trees with a higher probability as dead and the others as alive. The overall prediction accuracy of the model was 78%. A similar prediction accuracy was obtained when discolouration was used instead of dead branches (Nagelkerke's $R^2 = 0.39$, accuracy = 76%).

Trees with mistletoes were slightly larger and had significantly higher transparency, and more dead branches in 1998 (Table 5). Given the same transparency class, trees with medium and high mistletoe ratings suffered higher mortality rates than trees without or with low mistletoe rating (Fig. 1). While trees in the low transparency class with low mistletoe rating had no increased mortality rates, in the high transparency class trees with low mistletoe ratings suffered higher mortality than trees without mistletoes.

Trees in the subplot that survived until 2002 (40 trees) and the trees that were alive between 2000 and 2004 (34 trees, including three in-growth trees from 2000) were grouped into trees with mistletoes (mean mistletoe rating ≥0.5) and trees without (mean mistletoe rating <0.5). It should be noted that most trees with medium to high mistletoe ratings had died following the drought in 1997/1998 and 2003/2004 and were therefore excluded. At the beginning of the periods in 1996 and 2000 no significant differences in transparency were found between the groups of trees (1996 – trees without mistletoes: 15.2%, mistletoe trees: 12.5%, 2000 – trees without mistletoes: 31.8%, mistletoe trees: 33.5%). However, following the two drought periods the transparency of the trees with mistletoes was significantly higher than that of trees without mistletoes: in 2002 (trees without mistletoe: 22.7%, mistletoe trees: 34.4%) and in 2004 (trees without mistletoes: 22.1%, mistletoe

Table 2. **Number of trees and mortality rates for pines and non-pines between 1996 and 2004 and annual precipitation between the assessments in July (July previous year – June current year)**

	Alive	Mortality rates								
	1996	1996/ 1997	1997/ 1998	1998/ 1999	1999/ 2000	2000/ 2001	2001/ 2002	2002/ 2003	2003/ 2004	1996/ 2004
Precipitation (mm)		583	401	575	505	821	555	546	443	554
Pines, whole plot, N (%)	411	n.a.	32 (7.8)[1]	67 (17.7)[2]	48 (15.4)[3]	26 (9.8)	6 (2.5)	1 (0.4)	61 (26.4)	209 (58.6)
Pines, subplot, N (%)	74	0 (0)	4 (5.4)	21 (30)	4 (8.2)	5 (11.1)	1 (2.5)	0 (0)	8 (20.5)	43 (58.1)
Others, subplot, N (%)	40	1 (2.5)	1 (2.6)	3 (7.9)	0 (0)	1 (2.9)	0 (0)	0 (0)	0 (0)	6 (15.0)

[1] Mortality rate over 27 months.
[2] Assessed in April 1999.
[3] Assessed in June 2000.
n.a., not assessed.

Table 3. **Categorical logistic regression (variables, degrees of freedom, chi-square statistics and probability of significance, bold represents significance at the 95% confidence level)**

Source	d.f.	Chi-square	Probability
Intercept	**1**	**5.68**	**0.0172**
Transparency	**1**	**20.45**	**<0.0001**
Discolouration	1	2.65	0.1038
Dead branches	**1**	**7.23**	**0.0072**
Mistletoe rating	**3**	**26.02**	**<0.0001**
Tomicus shoot	1	0.04	0.8385
Male flowers	1	0.34	0.5619
Social position	4	1.46	0.8341
Diameter 1.3 m	1	0.67	0.4136
Crown shading	3	2.65	0.4483
Likelihood ratio	361	355.93	0.5654

Table 4. **Logistic regression with the significant parameters only (parameter estimates, SE, Wald chi-square test statistics, overall likelihood ratio statistics)**

Variable	d.f.	Parameter estimate	SE	Wald chi-square	p-value > χ^2
Intercept	1	3.434	0.393	76.42	0.0001
Transparency	1	−0.058	0.012	25.21	0.0001
Mistletoe rating	1	−1.008	0.193	27.33	0.0001
Dead branches	1	−0.146	0.039	14.21	0.0002

Log-likelihood test of the hypothesis ß = 0 was <0.0001 and Nagelkerke's R^2 statistics = 0.41.

Table 5. **Mean stem d.b.h., transparency and dead branch and twig percentage by mistletoe rating (Kruskal–Wallis test statistics: $p < 0.001$ for all three variables)**

Mistletoe rating	N	d.b.h. (cm)	Transparency (%)	Dead branches (%)
No	127	17.2	25.5	1.9
Low	187	18.2	28.5	3.0
Medium	51	20.5	40.4	6.6
High	14	22.4	46.4	9.5

trees: 29.1%). In most years the change in transparency was not significantly different ($p < 0.05$) between the groups as found by the Kruskal–Wallis test statistics. However, following a drought or in the second year of the drought, transparency increased significantly more in trees with mistletoes (1998/1999, 2003/2004, Fig. 2). On the other hand, in the year of the drought, respectively, the first year of the drought the opposite was found: trees with mistletoe had reduced transparency in comparison to trees without mistletoes (significant in 1997/1998, but not significant in 2002/2003, see Fig. 2). The correlation between the changes in crown transparency and the relative precipitation during that period (precipitation sum $\text{July}_{\text{year } t}$– $\text{June}_{\text{year } t+1}$ in percentage of the annual mean, see Fig. 2) was 0.82 for trees without mistletoe, but only 0.58 for trees with mistletoe, indicating the delayed response of trees with mistletoes to drought.

Finally, we used the trees that survived until 2003 to see if mistletoe infection or severity has changed over time (Fig. 3). Between 1996 and 2003 the number of infected trees increased from 38% in 1996 to 58% in 2003 and the mistletoe rating more than doubled from 0.38 in 1996 to 0.85 in 2003.

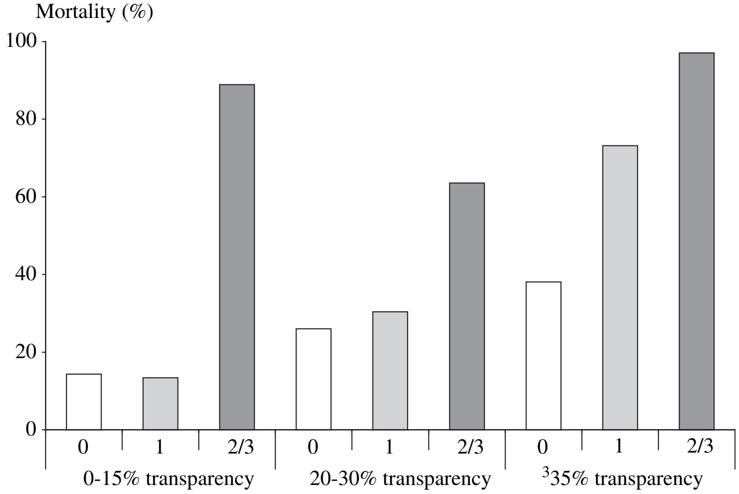

Fig. 1. Mortality 1998–2003 of Scots pines by transparency class and mistletoe rating in 1998 (0 = no, 1 = low, 2/3 = medium or heavy mistletoe infection)

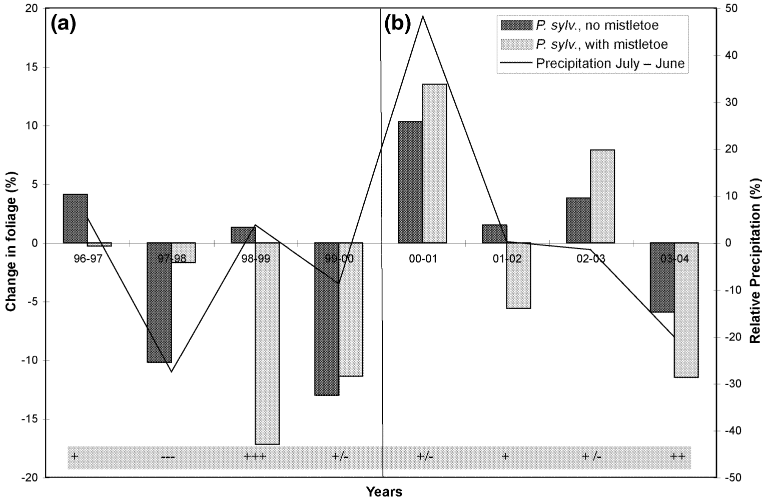

Fig. 2. Annual change in crown foliage (inverse of crown transparency) of surviving pines with and without mistletoes for (a) 1996–2000 (18 trees without and 22 trees with mistletoe) and (b) 2000–2004 (17 trees each) and relative deviation in precipitation sum ($\text{July}_{\text{year t}}$– $\text{June}_{\text{year t+1}}$) in percentage of the mean annual value 1996–2004 [no differences (+/–), increase (+) or decrease (–) in foliage of trees without mistletoe in comparison to trees with mistletoe; +, – = p-value ≤ 0.1; ++, – – = p-value ≤ 0.05; +++, – – – = p-value ≤ 0.01]

4 Discussion

The mortality rates of the pines at the LWF site Visp are higher than mortality rates reported at other sites in Valais (Rigling and Cherubini 1999; Dobbertin et al. 2005b).

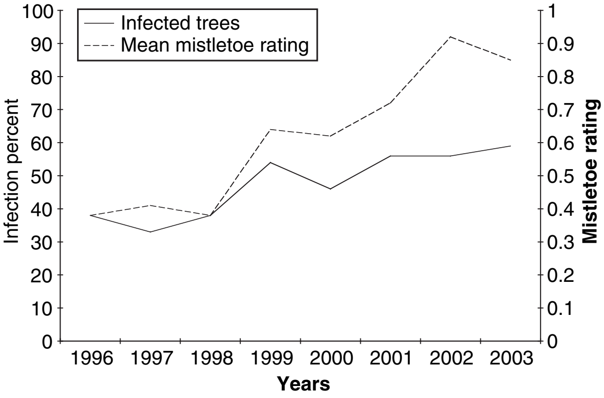

Fig. 3. Trend in percentage of mistletoe infected trees and mistletoe ratings of surviving pines between 1996 and 2003

Mortality was highest following years of drought, such as 1998, 2003 and 2004. Although total precipitation from July 2002 to June 2003 was more than 550 mm, spring and summer 2003 were extremely dry, and the summer 2003 was the warmest ever measured (5°C above the long-term mean 1961–1990, Schär et al. 2004). Drought is a common inciting stress factor, which may lead to tree mortality in subsequent years. Pedersen (1998) found that drought stress resulted in decreased stem growth of oaks and occurred often decades before tree death. Oberhuber (2001) also reported that drought coincided with subsequent stem growth decrease in Scots pine years prior to tree death. He also found that pine mortality was highest on shallow soils with low water-holding capacity.

The finding in our study that deciduous trees had mortality rates of one-fourth of that of the pines confirms the findings of a previous study on the systematic 1 × 1-km grid of the Swiss National Forest Inventory (NFI) between 1983 and 2003 (Dobbertin et al. 2005b). Higher pine mortality in comparison with other species, such as downy oak (*Q. pubescens*) and whitebeam (*S. aria*) may be either due to a higher drought tolerances of these species (Weber 2005; Zweifel et al. 2005) or other pine-specific contributing factors, such as insects (i.e. various bark beetles, Rigling and Cherubini 1999) or pine wood nematodes (Polomski et al. 2006). Drought decreases the resistance of stressed trees and warm weather provides favourable conditions for the development of insect populations (Mattson and Haack 1987; Berryman 1989). On dying pines in spring 1999 galleries of *P. cyanea* were commonly found. However, no beetle species could be identified as the main cause of the mortality (B. Forster, personal communication). Tsopelas et al. (2004) observed in Greece that a buprestidae beetle (*P. knoteki*) appeared to be a contributing factor to tree mortality of silver fir (*Abies alba* Mill.) infected by *V. album* ssp. *abietis*.

Crown transparency percentage, mistletoe rating and dead branch percentage were significant factors in a multivariate categorical regression model. Prediction accuracy of correct dead and alive trees were equal or higher than reported in other similar studies (Gottschalk et al. 1998; Negron 1998), indicating the usefulness of the assessed variables. Transparency has been successfully used as predictor of subsequent mortality for other species in Switzerland (Dobbertin and Brang 2001). The relationship between transparency and mortality either indicates a predisposing condition of the tree or that trees have been affected by an unknown factor causing increased needle fall and subsequent tree death.

At the site Visp crown transparency in 1996 also correlated with tree mortality following the drought of 1998 (data not shown) and drought could be identified as the inciting factor at Visp (Dobbertin et al. 2005b). It can therefore be hypothesized that crown transparency at Visp is an indicator of reduced tree vitality, whose causes are not known yet. None of the tree size or competition measures was significant, indicating that competition for light and resources was not a major predisposing factor as is usually the case for shade-intolerant species (Dobbertin and Biging 1998). As mistletoe infestation was higher in larger and open-grown trees, it is possible that the negative effect of mistletoes confounds the effect of competition.

Mistletoe rating was found to be highly significant in our mortality model. Given the same crown transparency, trees with medium and high mistletoe ratings had much higher mortality rates than trees with no or low mistletoe ratings. In a mortality model for *P. ponderosa* dwarf mistletoe (*Arceuthobium campylopodum*) density was highly significant, in addition to tree density (i.e. basal area), with mistletoe density being the stronger factor (Roth 2001). Mortality of silver fir in Greece, following drought correlated significantly with infections by the mistletoe *V. album* ssp. *abietis* (Tsopelas et al. 2004). In a fertilizer experiment in northeastern Oregon, *Larix occidentalis* with severe dwarf mistletoe (*A. laricis*) infection had 10-year mortality rates of 56%, trees with moderate infections had 10% and trees without or with very light infection had no mortality (Filip et al. 2002). In Nevada increasing mortality of *Acacia greggi* after drought correlated with increasing severity of *Phoradendron californicum* infection (Lei 2001). At high altitude sites in Arizona 3-year mortality rates for *Picea pungens* with high mistletoe (*A. microcarpum*) infection were 19% when compared with mortality rates of <3% for trees with low infection rates (Lynch 2004). In one study Douglas-fir (*Pseudotsuga menziesii*) stands that were severely infected with *A. douglasii* had three to four times higher mortality rates than stands with low infection rates (Mathiasen et al. 1990), while in another study two to three times higher mortality rates were found (Lundquist et al. 2002). In a survey in 2002/2003 on 153 Swiss NFI plots, Scots pines classified as 'damaged' by mistletoe in the first or second NFI (1983–1985, 1993–1995) had mortality rates two to three times higher than those pines not classified as 'damaged' (Dobbertin et al. 2005a).

Very few experimental studies have been carried out to test if mistletoe infection increased tree mortality. While Reid et al. (1992) failed to prove a significant treatment effect of the experimentally induced mistletoe *Amyema preissii* on the survival of *Acacia victoriae* in Australia, they found a significant effect of mistletoe volume on mortality. However, a paired removal experiment of *Amyema miquelii* mistletoes on two *Eucalyptus* hosts in Australia found significant higher mortality and reduced growth and foliage mass in the control group after only 33 months (Reid et al. 1994).

In our study, mistletoe intensity correlated also positively with crown transparency, which is in accordance with other studies (Meining et al. 2004). The possible reasons for this correlation could be that: (i) mistletoes in transparent trees are more visible, (ii) mistletoes as light-demanding species grow better in more transparent tree crowns, (iii) trees weakened by an unknown factor react with increased crown transparency and at the same time are more susceptible to mistletoe infections or (iv) mistletoe causes premature needle fall. Although crown density may influence the detection of mistletoes in the crown, Scots pine crowns are usually fairly transparent allowing a relative accurate mistletoe recognition. It is known that *V. album* is a shade-intolerant species (Zuber 2004), therefore growth rates can be expected to increase with increasing light condition in more transparent tree crowns. Mistletoe may also profit from weakened condition of its host trees, but no clear scientific evidence has yet been presented (Hofstetter 1988). Hartmann (1990) found that new pine mistletoe infections were higher in years of drought stress. However, shoot regrowth of *A. vaginatum* dwarf mistletoe on *P. ponderosa* following experimental removal in Arizona was associated with better physiological condition of the host (BICKFORD et al. 2005), indicating that mistletoes are profiting from good host conditions. Although it cannot be ruled out that trees of poor vigour are predisposed to mistletoe infections, it is more likely that mistletoe infection is the cause of the reduced vigour. The findings in our study that trees without and with low mistletoe infection rates had very similar transparency rates, while trees with medium to high rates had much higher scores, and that transparency of infected trees increased following drought suggest that mistletoe is causing the needle loss. *Viscum album* ssp. *austriacum* had been found to have a three times lower water-use efficiency than its host *P. sylvestris* (SCHULZE et al. 1984) explaining possible negative effects on trees during drought. In a study on silver fir in Switzerland infected with *V. album* ssp. *abietis* no differences in the proportion of trees with a negative growth trend between uninfected trees and infected trees was found prior to the infection, but following the infection significantly more declining growth trends were found in infected trees (NÖTZLI et al. 2003).

Viscum album infection can therefore be considered both, as predisposing factor by increasing needle loss and thus reducing the tree's photosynthetic capacity and predisposing it to subsequent stress factors, and as contributing factor by increasing water stress during drought.

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Résumé

Le gui du pin (Viscum album ssp. austriacum) contribue à la mortalité des pins sylvestres (Pinus sylvestris) dans la vallée du Rhône en Suisse

Une forte mortalité des pins sylvestres (*Pinus sylvestris*) a été observée ces dernières années dans la vallée du Rhône en Suisse. Les causes exactes n'en sont pas connues. La mortalité des arbres et l'état des houppiers ont été suivis depuis 1996 dans une parcelle de 2 ha. Entre 1996 et 2004, 59% des pins sylvestres sont morts, la plupart après les périodes de sécheresse de 1996–98 et 2003–2004, comparé à 15% pour les feuillus. La transparence des houppiers, le jaunissement des aiguilles, le pourcentage de mortalité de branches, une note d'importance du gui (*Viscum album* ssp. *austriacum*), les attaques d'alimentation sur pousses par *Tomicus* sp., la floraison mâle, le diamètre du tronc, l'ombrage du houppier et le statut social des arbres, mesurés en 1998, ont été utilisés dans un modèle de régression logistique pour prédire la mortalité des arbres. La transparence des houppiers, le taux de gui et le pourcentage de branches mortes sont des variables significatives, dont l'augmentation est associée à une augmentation de la probabilité de mortalité des arbres. Le jaunissement des aiguilles pourrait être substituée à la mortalité des branches comme variable prédictrice. Tandis que la transparence des houppiers augmente avec le taux de gui, au sein de la même classe de transparence, les arbres avec une infestation de gui moyenne à forte ont une probabilité de mortalité 2 à 4 fois plus élevée que les arbres à infestation faible ou nulle. Chez les arbres survivants, on observe que les arbres porteurs de gui ont une augmentation plus forte de la transparence du houppier l'année suivant une sécheresse que les arbres sans gui, l'inverse étant vrai pendant une année sèche. La différence de transparence des houppiers entre arbres porteurs de gui et arbres sans gui n'était pas significative au début des observations, alors qu'à la fin de la période, les arbres avec gui ont une transparence plus forte. Nous concluons que l'infestation par le gui peut être considérée à la fois comme un facteur prédisposant à la mortalité, en augmentant la perte d'aiguilles après sécheresse, et un facteur contribuant, en augmentant le stress hydrique pendant la sécheresse.

Zusammenfassung

Die Mistel (Viscum album ssp. austriacum) trägt zum Absterben der Kiefern (Pinus sylvestris) im Schweizer Rhonetal bei

Seit einigen Jahren werden im Schweizer Rhonetal hohe Absterberaten der gemeinen Kiefer (*Pinus sylvestris* L.) beobachtet. Die genauen Ursachen sind bis jetzt unbekannt. Auf der zwei Hektar grossen langfristigen Waldökosystemfläche (LWF) Visp werden seit 1996 jährlich Absterberaten, Kronenverlichtung, Mistelbefall (*Viscum album* ssp. *austriacum*) und andere Symptome aufgenommen. Zwischen 1996 und 2004 sind 59% aller Föhren auf der Fläche abgestorben, die meisten nach den Trockenperioden 1996–98 und 2003–2004. Dagegen starben nur 15% der Laubbäume ab. Kronenverlichtung, Nadelverfärbung, Totast- und Totzweiganteil (als Indikatoren der Vitalität des Baumes), Mistelbefallsklasse, Triebabwurf durch Waldgärtner, männliche Blütenbildung, Stammdurchmesser, Kronenkonkurrenz und soziale Stellung, alle im Jahr 1998 erhoben, wurden in einer logistischen Regression zur Bestimmung der Absterbewahrscheinlichkeit auf Signifikanz getestet. Kronenverlichtung, Mistelbefallsklasse und Totastanteil waren in dem Model signifikant. Die Wahrscheinlichkeit des Absterbens stieg dabei mit ansteigender Kronenverlichtung, ansteigendem Mistelbefall und ansteigendem Totastanteil. Der Totastanteil konnte im Model durch die Nadelverfärbung ersetzt werden. Die Kronenverlichtung stieg mit dem Mistelbefall an. Bei gleicher Verlichtung starben jedoch Bäume mit mittlerem und starkem Mistelbefall zwei- bis viermal häufiger ab als Bäume ohne oder mit leichtem Mistelbefall. Von den überlebenden Bäumen zeigten solche mit Mistelbefall einen deutlichen Anstieg der Transparenz im Jahr nach Beginn der Trockenheit im Vergleich zu den Bäumen ohne Misteln, während im Jahr der Trockenheit das Umgekehrte der Fall war. Zu Beginn der Beobachtung ergaben sich keine signifikanten Unterschiede in der Kronentransparenz der überlebenden Bäume mit und ohne Misteln. Am Ende der Beobachtungsperiode wiesen jedoch die Bäume mit Misteln signifikant höhere Kronenverlichtungen auf. Wir schliessen daraus, dass die Misteln auf der einen Seite den Baum langfristig schwächen, indem sie zur Reduzierung der Nadelmasse führen und sie auf der anderen Seite während Trockenheit durch erhöhten Wasserstress zum vorzeitigen Absterben beitragen.

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