

Mistletoe-induced crown degradation in Scots pine in a xeric environment

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Summary Increasing Scots pine (*Pinus sylvestris* L.) mortality has been recently observed in the dry inner valleys of the European Alps. Besides drought, infection with pine mistletoe (*Viscum album* ssp. *austriacum*) seems to play an important role in the mortality dynamics of Scots pines, but how mistletoes promote pine decline remains unclear. To verify whether pine mistletoe infection weakens the host via crown degradation, as observed for dwarf mistletoes, we studied the negative effects of pine mistletoe infestation on the photosynthetic tissues and branch growth of pairs of infested and non-infested branches. Pine mistletoe infection leads to crown degradation in its host by reducing the length, the radial increment, the ramification, the needle length and the number of needle years of the infested branches. This massive loss in photosynthetic tissue results in a reduction in primary production and a subsequent decrease in carbohydrate availability. The significant reduction in needle length due to mistletoe infection is an indication for a lower water and nutrient availability in infested branches. Thus, mistletoe infection might lead to a decrease in the availability of water and carbohydrates, the two most important growth factors, which are already shortened due to the chronic drought situation in the area. Therefore, pine mistletoe increases the risk of drought-induced mortality of its host when growing in a xeric environment.

Keywords: climate change, crown architecture, drought, forest decline, inner Alps, *Pinus sylvestris* L., *Viscum album* ssp. *austriacum*.

Introduction

Mistletoes are hemiparasites depending completely on their host tree for water and nutrient supply (Popp and Richter 1998, Watson 2001, Zuber 2004). Mistletoes, in general, have lower water use efficiency than the host due to much higher transpiration rates and stomatal conductance and lower

leaf water potential (Mathiasen et al. 2008). Thus, mistletoes increase the drought stress of the host (Glatzel and Geils 2009).

Although capable of fixing atmospheric carbon, mistletoes also extract carbon from the xylem sap of the host, resulting in partial heterotrophy (Marshall et al. 1994, Popp and Richter 1998, Escher et al. 2004). This might additionally contribute to a weakening of the host under limiting growing conditions.

The European mistletoe (*Viscum album*) is divided into four subspecies with different host species (Zuber 2004). One subspecies is the pine mistletoe (*Viscum album* ssp. *austriacum*) with trees from the genus *Pinus* as main hosts. All subspecies are highly temperature sensitive (Tubeuf et al. 1923, Skre 1979). Low summer and low winter temperatures are limiting their dissemination (Iversen 1944, Skre 1971, 1979). Consequently, pine mistletoes are expected to profit from ongoing climate changes by increasing their geographical ranges. This was already shown for the Swiss Rhone Valley where pine mistletoes have shifted 200 m to higher altitudes due to warming during the past century (Dobbertin et al. 2005a).

In dry inner valleys of the European Alps, Scots pine (*Pinus sylvestris* L.), the host of pine mistletoe, recently showed a considerable increase in mortality rates [e.g., in the Swiss Rhone Valley (Dobbertin et al. 2005b, Bigler et al. 2006), the Italian Aosta Valley (Vertui and Tagliaferro 1998, Dobbertin et al. 2005b) and the Austrian Inn Valley (Oberhuber 2001)]. Mortality rates were highest after drought years on dry sites (Dobbertin et al. 2005a). Locally, up to 50% of the population died (Rebetez and Dobbertin 2004). Comprehensive studies revealed multiple stress factors being involved in this pine decline, such as drought (Rigling and Cherubini 1999, Dobbertin 2005, Bigler et al. 2006, Weber et al. 2007, Eilmann et al. 2009, Zweifel et al. 2009), insects (Wermelinger et al. 2008), pathogens (Giordano et al. 2009), nematodes (Polomski et al. 2006), stand competition (Weber et al. 2008) and also mistletoe (Dobbertin and Rigling 2006). Pines infested by mistletoe showed a two to four times higher probability of dying than non-infested trees. The negative impact

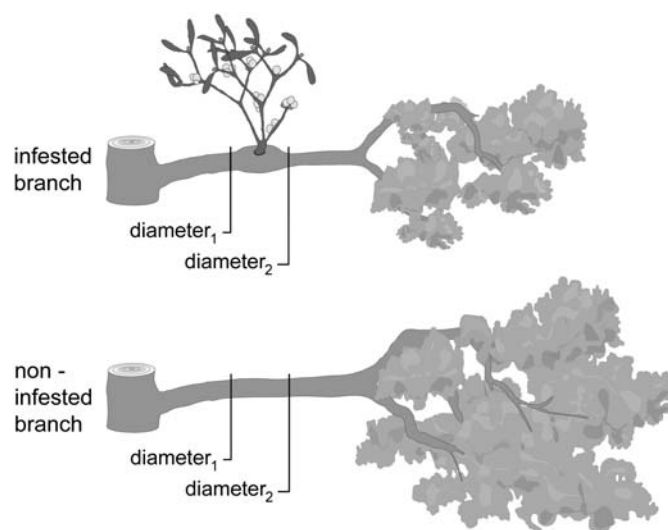


Figure 1. Scheme of sampling in infested and non-infested branches.

of these factors on pine performance was greatest in poor-looking trees with transparent crowns and low needle mass—trees with fully foliated crowns were shown to be less susceptible to those stress factors (Dobbertin and Rigling 2006, Wermelinger et al. 2008, Eilmann 2009). So far, it remains unclear whether pine mistletoe infestation is responsible for the degradation of the pine crowns, making them more susceptible to additional stress factors as suggested for dwarf mistletoes by, e.g., Hawksworth et al. (1983), Geils and Hawksworth (2002) and Mathiasen et al. (2008).

The aim of this study was to quantify the impact of pine mistletoe infection on crown architecture of Scots pine. Hence, we measured several growth parameters including branch size and needle mass separately for mistletoe-infested and non-infested branches of the same trees. The objectives were to validate the following hypotheses:

- I. Pine mistletoe infection leads to changes of the crown architecture of the infested Scots pines.
- II. Pine mistletoe infection reduces the photosynthetic active tissue, as needle mass and needle size will be decreased.

Materials and methods

Study site and sampling

The study was realized in the two main damage areas in the Swiss Rhone Valley where mortality rates were highest (Wermelinger et al. 2008). One site (46°14' N, 07°52' E) was located above the village of Stalden in a side valley of the Swiss Rhone Valley. The site is situated at 900 m a. s. l. on a west-exposed slope with 50% incline. The forest is dominated by 50- to 170-year-old Scots pine with only few deciduous trees mixed in. The average tree height was 9 m. The second site (46°19' N, 07°34' E) was situated near the village

of Salgesch in the main valley, 25 km away from Stalden. The site is situated at 900 m a. s. l. on a south-exposed slope with 50% incline. The stand consisted mainly of 80- to 180-year-old Scots pine, again mixed with some deciduous trees. The average tree height was 10 m. On both sites, the soil type can be consistently described as Rendzic Leptosol with limestone as parent material. Annual precipitation of the nearest climate stations ranges between 530 and 650 mm and mean annual temperature is estimated at 7.3 °C.

For the sampling in February 2005, nine trees per site were randomly selected. These trees were dominant and showed a similar crown condition, estimated by crown transparency assessment. Due to the similarity of the trees, a possible effect of the individual tree on the growth response of the branches to mistletoe infection can be regarded as negligible. Depending on crown length, up to three pairs of branches (one infested, one non-infested) per tree were cut from the upper part of the crown. Twenty-nine pairs of branches were selected on both sites: 13 in Stalden and 16 in Salgesch. The branch pairs were selected using the following restrictions for the infested branches: (i) only one mistletoe per branch (no multiple mistletoe infections) and (ii) a minimal distance between mistletoe and the stem of 20 cm to avoid that diameter₁ (see Figure 1) will be influenced by the knot roots. To avoid a bias by the typical swelling caused by hypertrophy of the host tissue due to mistletoe infection (Mathiasen et al. 2008), diameter₁ in infested branches was measured 10 cm before the point of infection. The age and mass of the mistletoe was not a criterion for selection, and therefore, differed between the infested branches. The non-infested branch originated from the same whorl and was similar to the infested branch with respect to diameter₁.

To obtain a longer needle length time series, additional mistletoe-infested and non-infested branches from the same two sites, but felled in 2002, were added. Altogether, 50 branch pairs (24 from Salgesch and 26 from Stalden) were used.

Table 1. Mean values of various growth parameters in infested and non-infested branches. All growth parameters, except for branch diameter, were measured after diameter₂. The differences between infested and non-infested branches were tested with the Wilcoxon sign rank test (*P*-value). Needle plus mistletoe dry mass in infested branches was tested against needle dry weight in non-infested branches.

	Non-infested branches	Infested branches	<i>p</i> -value
Branch diameter ₁ [cm]	10.6	10.8	n.s.
Branch diameter ₂ [cm]	9.1	6.1	<0.001
Branch length [cm]	46.1	33.7	<0.001
Needle length [mm]	27.0	21.6	<0.001
Needle width [mm]	1.4	1.2	<0.001
Needle dry weight [g]	26.6	6.2	<0.001
Needle plus mistletoe dry weight [g]		23.7	n.s.
Branching [count]	37.9	10.4	<0.001
Cones [count]	2.9	0.4	<0.01
Needle generations [count]	4.2	2.9	<0.001
Tree rings [count]	14.2	11.1	<0.001

Measurements

To analyse the effect of mistletoe infection on the branch architecture, growth parameters were measured at or after diameter₂, located 10 cm distal to the mistletoe and at the corresponding place (20 cm distal to diameter₁) in the case of non-infested branches (see Figure 1). We counted the number of branching and tree rings and measured branch diameter and branch length. To gather information on whether mistletoe infection affected the potential of regeneration, the number of cones per branch was counted. The impact of mistletoe infection on the photosynthetic tissue was evaluated by counting the number of needle generations per branch and by measuring needle geometry and green biomass. To analyse needle geometry, we selected 20 fresh needles per branch and needle generation and scanned them with a distortion-free scanner (Color Scanner Expression 1000 XL, 12 000 dpi; Epson, Long Beach, CA). The length and width of the needles were automatically measured with the software WinSeedle (Regents Instruments Inc., Canada) and mean values per year were calculated. In order to assess whether the effect of mistletoe infection on needle length intensified in drought years, we compared annual needle length with climate data (precipitation sum of the months February to April with data coming from the weather station in Ackersand; at 2 km distance from the site in Stalden and at 23 km distance from the site in Salgesch). To analyse the green biomass, all needles of a branch and, in the case of infested branches, also the whole mistletoes were dried for 48 h at 60 °C and weighed.

For all analysed growth parameters, we first applied an analysis of covariance (ANCOVA) with location and infection (infested or non-infested) as factors and branch diameter₁ as covariate. The results gave no statistically significant effect of the location and its interactions. Therefore, we pooled the growth parameters of the two sites and tested the differences in branch growth due to mistletoe infection using the paired Wilcoxon signed-rank test.

To analyse the impact of mistletoe infection on radial increment, we analysed the difference in tree-ring width between diameter₁ and diameter₂ in infested and also in non-infested

branches. Therefore, we cut two discs per branch. The discs were sanded and tree-ring width was measured on the upper side of the discs on two radii per disc avoiding compression wood. For the measurements, a Lintab digital positioning table and the software TSAP (both Rintech, Heidelberg, Germany) were used. The two measurements per disc were cross-dated and averaged to a mean. The calculation of an average curve per tree, site or treatment (infested vs. non-infested) is not permissible as the infection date varied strongly between the branches since new infections can occur every year. As the measured tree-ring series were rather short, no cross-dating between the different branches was possible. Hence, missing rings were detected but the tree-ring series not correspondingly corrected, resulting in an underestimation of the negative impact of mistletoe on radial growth (Figure 4).

Results

Mistletoe infection had a strong impact on branch architecture, as growth was significantly limited in infested branches (Table 1). Diameter₁ before mistletoe infection showed no statistically significant differences indicative of the paired sampling of similar-sized branches. Branches infested by mistletoe were reduced by 33% in diameter₂, by 27% in length and by 72% in ramification. The number of tree rings was reduced by 22%. Also, the amount and shape of the needles decreased due to mistletoe infection (needle mass –77%, needle length –20% and needle width –9%). Thirty percent fewer needle generations and 87% fewer cones were found in infested branches.

The relationship between green biomass and branch basal area at diameter₁ (Figure 2) was generally very strong, as seen by the highly significant regression and high *R*². However, in infested branches, *R*² was considerably lower when only regarding the needle mass. Per unit basal area, fewer needles were supported by the branch. In non-infested branches, needle mass was almost equal to the sum of needle mass and the mass of the mistletoe in infested branches, but

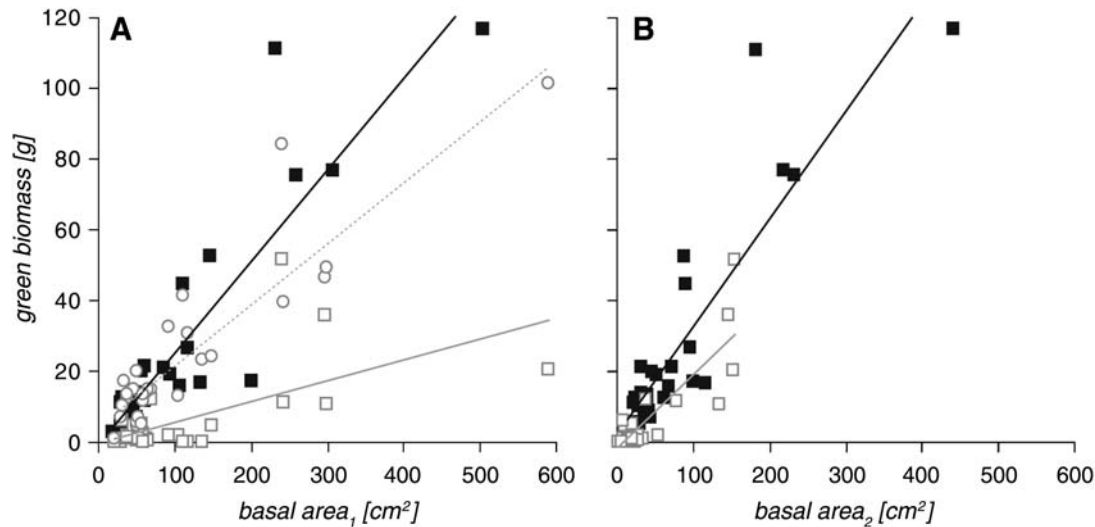


Figure 2. Green biomass vs. basal area at diameter₁ (A) and at diameter₂ (B). Closed squares, needle mass of non-infested branches (black regression line: (A) $y = 0.2583x - 0.7364$, $R^2 = 0.801$, $P < 0.001$; (B) $y = 0.304x + 2.298$, $R^2 = 0.7993$, $P < 0.001$); open squares, needle mass of infested branches (grey solid regression line: (A) $y = 0.0589x - 0.4371$, $R^2 = 0.3754$, $P < 0.001$; (B) $y = 0.2098x - 1.9078$, $R^2 = 0.7155$, $P < 0.001$); open circles, needle mass plus mistletoe mass of infested branches (grey dashed regression line: (A) $y = 0.1724x + 4.371$, $R^2 = 0.8153$, $P < 0.001$).

still, on average, less needle/leaf mass was supported in infested branches. When comparing basal area at diameter₂ against needle mass, the R^2 for the regression between basal area and needle mass increased substantially in infested branches and remained identical in non-infested branches (Figure 2). Again, the slope was smaller for infested branches.

The variation of needle length per year (Figure 3) coincided with the developing of late winter/spring precipitation

(February to April), as needle length increased with increasing precipitation. This was most pronounced on the site near Salgesch. On the site near Stalden, a deviation from the development of precipitation was found in the year 1999. Consistently for both sites, needle length was significantly lower in infested branches compared with non-infested branches. However, the negative effect of mistletoe infection on needle length did not differ between dry and moist years.

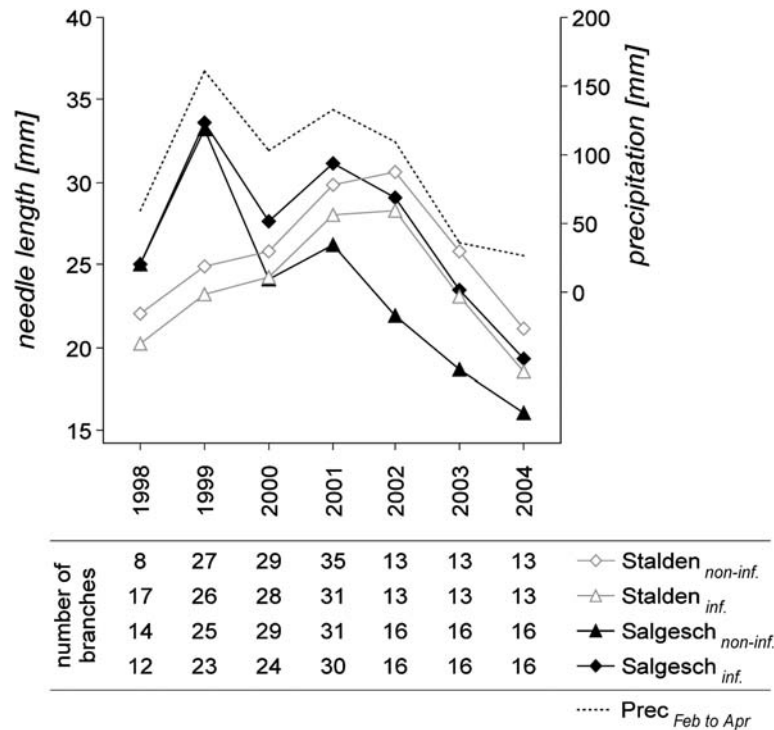


Figure 3. Developing of the mean annual needle length together with late winter/spring precipitation (Prec_{Feb to Apr}) separately for the two sites and for infested and non-infested branches.

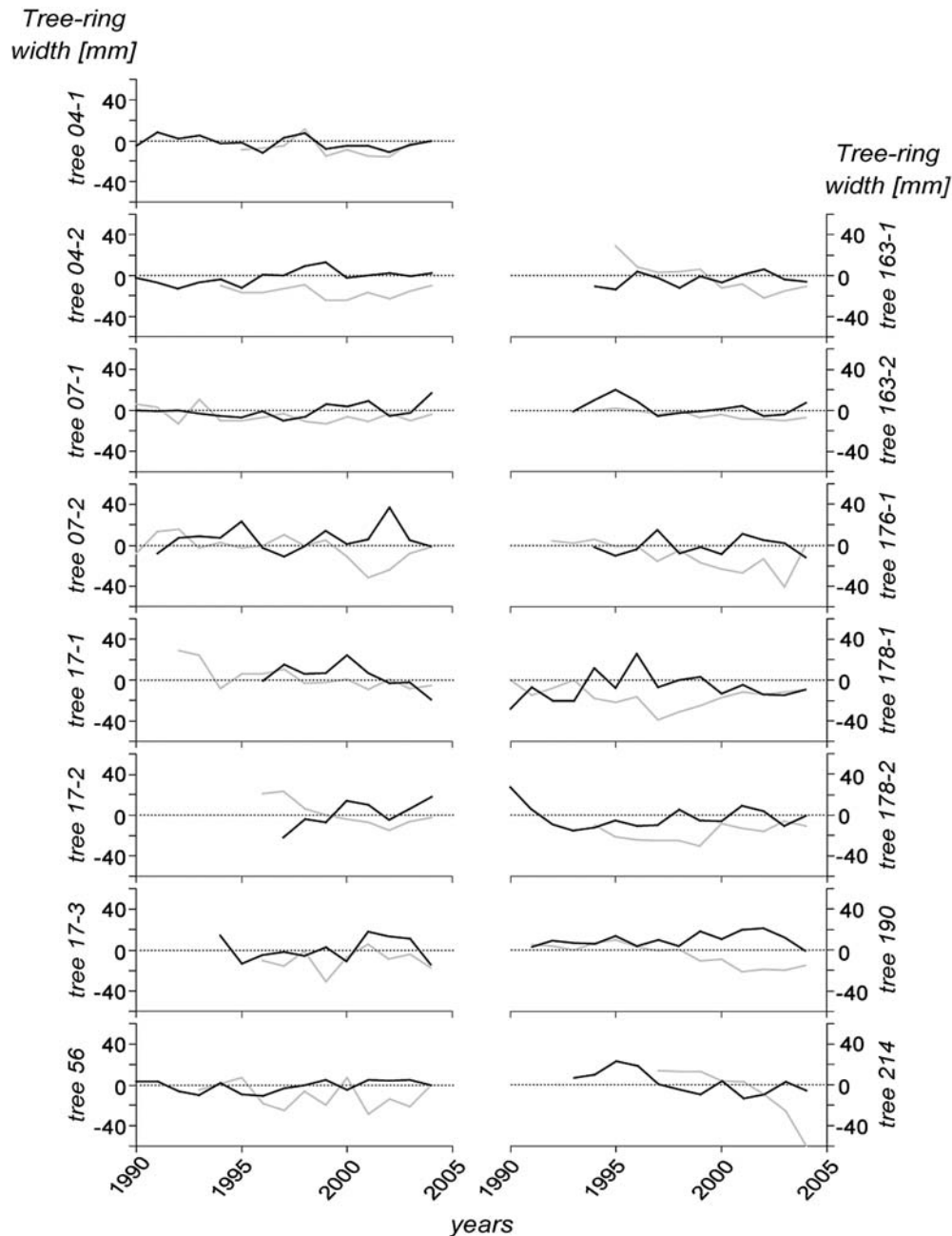


Figure 4. Difference of tree-ring width at branch diameter₂ minus branch diameter₁ in infested (grey) and non-infested branches (black) using the example of the Salgesch site (drought years 1996, 1998, 2003 and 2004).

Comparing the differences between tree-ring widths at branch diameter₂ minus diameter₁ (Figure 4), more negative values were found in infested branches, underlining the impairment of growth after the point of infection [non-infested branches: $\text{mean}_{\text{stalden}} = -0.47$ (1/100 mm), $\text{mean}_{\text{salgesch}} = 0.11$; infested branches: $\text{mean}_{\text{stalden}} = -6.60$ (1/100 mm), $\text{mean}_{\text{salgesch}} = -5.19$]. The start of mismatching between the curves was individual but the occurrence of negative values in infested branches increased with time.

No significant differences (ANCOVA, data not shown) in the response to mistletoe infection were found between the

sites. Only for tree-ring width, slight but non-significant differences between the sites existed (Figure 4), as a stronger effect of mistletoe infection was found on trees in the south-exposed site (Salgesch).

Discussion

Pine mistletoe infection led to a degradation of the crown via a significant reduction in branch size, ramification and needle measures (Table 1). In addition, the number of cones was sig-

nificantly reduced. Hence, pine mistletoe has a similar negative effect on its host to that observed for dwarf mistletoes (Hawksworth et al. 1983, Tennakoon and Pate 1996, Geils and Hawksworth 2002, Mathiasen et al. 2008).

The total photosynthetically active tissue of branches was not significantly reduced by mistletoe infection as needle mass of non-infested branches was nearly equivalent to needle mass plus mistletoe mass of infested branches. Hence, mistletoe mass was similar to the amount of shed pine needles (Table 1 and Figure 2). However, when comparing only needle mass and, therefore, the photosynthetic active tissue of Scots pine, the destructive impact of mistletoe becomes visible as needle mass in branches of similar diameter was reduced by 77% due to the infection. This is in accordance with the results of Reid et al. (1994) for box mistletoe infection on *Eucalyptus* species and with the results of Dobbertin and Rigling (2006) showing increasing crown transparency due to pine mistletoe infection.

The high correlation of needle mass with basal area in non-infested branches and of needle mass plus the mistletoe mass with basal area in infested branches (Figure 2) indicates that the area of water-conducting xylem determines the amount of supported foliage according to the pipe model theory (Shinozaki et al. 1964). However, regarding the total needle mass, less foliage was supported per branch basal area in infested branches than in non-infested branches. There are two possible explanations for this. First, even after mistletoe infestation needle mass has declined, an equilibrium between water-conducting area and foliage has not yet been reached. However, the date of mistletoe infection varied between the branches as pine mistletoe infection is not related to climatic events, but to regular propagation by birds. Therefore, the imbalance between water-conducting area and foliage should not be found in branches with very old mistletoe. A second explanation might be that less water is available in infested branches past the mistletoe infestation point than in non-infested branches of similar diameters. In other words, more xylem is needed to support the same amount of foliage. In both cases, the negative effect of the mistletoe is obvious.

Mistletoes show much higher transpiration rates and lower water potential than the host trees (Marshall et al. 1994, Popp and Richter 1998, Mathiasen et al. 2008). As a result, xylem hydraulic conductivity distal to the point of infection can be considerably reduced, leading to a premature shedding of needles or in the end to branch die-back (Mathiasen et al. 2008). Therefore, the reduction in needle mass found in our study might be a result of increasing drought stress due to mistletoe infection.

Due to the low needle mass, infested branches should be barely able to substantially contribute to whole-tree primary production. This negative effect on carbon fixation is reinforced by the reduction in photosynthetic rate of the host (Mathiasen et al. 2008, Glatzel and Geils 2009) and the extraction of carbohydrates from the xylem sap of the host by mistletoe (Popp and Richter 1998, Watson 2001, Escher et al. 2004). Thus, besides the increase in drought stress by mistle-

toe infection, the reduction in carbohydrate availability might be an additional limiting factor contributing to increased mortality risk during drought years in infested trees (Dobbertin and Rigling 2006).

Not only the number of needles, but also their length and width were significantly reduced by mistletoe infection. Generally, needle length was closely related to water availability in late winter/spring (February to April) in infested and non-infested branches: it was reduced when precipitation was low and increased with increasing precipitation (Figure 3). Shorter needles under drought were also observed in previous studies on *Pinus* sp. (Irvine et al. 1998, Lebourgeois et al. 1998, Cinnirella et al. 2002, Grill et al. 2004, Dobbertin et al. 2010). Dobbertin et al. (2010) showed that irrigation of mature Scots pines in the vicinity of this study increased needle length by up to 70%. They also showed that needle length in both irrigated and controlled trees correlated with spring water availability. The reduction in needle length due to mistletoe infection might be again a result of the mistletoe-induced increase in drought stress reducing the water availability for needle elongation distal to the mistletoe. However, an amplifying effect of mistletoe infection during drought was unapparent, as needle length was not more reduced in drought years. The differences between infested and non-infested branches were constant between the years.

Also, wood formation was limited by mistletoe infection as the number of tree rings was considerably reduced, resulting in a higher number of missing tree rings distal to the mistletoe. No tree rings are built if the amount of available carbohydrates is too low due to unfavourable growth conditions to stimulate cambial activity (missing rings). Therefore, the number of missing rings can be seen as proxy for growth limitation (Fritts 2001, Cherubini et al. 2002, Rigling et al. 2004).

Regarding tree-ring width, the subtraction of diameter₁ from diameter₂ (Figure 1), which are only 20 cm apart from each other, should result in values around 0, as seen for non-infested branches [mean = -0.47 (1/100 mm) or 0.11] in Figure 4. But infested branches showed negative values [mean = -6.60 (1/100 mm) or -5.19], demonstrating the negative effect of mistletoe infection on annual increment. Thus, the smaller branch diameter distal to the mistletoe was due to both a higher number of missing rings and a reduction in tree-ring width. The drop in increment cannot be triggered by mistletoe infection as (i) the time of mistletoe infection varied between the branches and (ii) mistletoe starts growing very slowly after infestation with almost no impact on the host tree but exponentially increasing its growth rates after some years (Noetzli et al. 2003). Therefore, based on data on branch growth, an exact reconstruction of mistletoe age or of the date of the infection is impossible. Consequently, we are convinced that rather the negative impact of drought (Rigling et al. 2003, Weber et al. 2007, Eilmann et al. 2009) accentuated by the high water consumption of mistletoe (Marshall et al. 1994, Popp and Richter 1998, Mathiasen et al. 2008) resulted in a cumulative effect on tree growth. This cumulative negative impact of drought

and mistletoe infection on the performance of the tree might contribute to higher mortality rates in mistletoe-infested pines after drought years (Dobbertin and Rigling 2006).

Conclusions

According to our results, both hypotheses can be approved as mistletoe clearly alters the crown architecture of Scots pine, resulting in a significant reduction in photosynthetically active tissue. Thus, mistletoe infection diminishes carbohydrate availability not only directly by extracting carbohydrates from the xylem sap but also indirectly via branch and needle mass reduction. In addition, mistletoe infection increases drought stress, as seen in the reduction of needle mass and needle length, two parameters that are expected to respond directly to water availability. Thus, in this dry environment, mistletoe infection reinforces the negative effects of drought on tree growth by further decreasing both carbohydrate and water availability, making its hosts more susceptible to decline.

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