Analysis of *Cronartium flaccidum* Lesion Development on Pole-stage Scots Pines

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Kaitera, J. 2000. Analysis of *Cronartium flaccidum* lesion development on pole-stage Scots pines. Silva Fennica 34(1): 21–27.

Historical and current lesion development and sporulation of *Cronartium flaccidum* was investigated in a stand of artificially seeded pole-stage *Pinus sylvestris* in northern Finland. An average of 6.5 lesions developed per infected tree, most of them occurring on a minority (25 %) of the trees. During the monitoring period of five years, fresh aecia appeared mainly in 7–10-year-old shoots, the age of the shoots bearing aecia varying between 3–20 years. Aecia appeared for the first time most frequently in 5–10-year-old shoots. Infection waves occurred, whereas lesions were formed most frequently in shoots formed in various years through the 1980s. After the lesions started to sporulate, sporulation in most lesions that finished sporulating during the monitoring period lasted for 1–2 years. The aecia in between 47 % and 59 % of the infected shoots developed annually over a longer length in proximal direction than in distal direction next to the previous year's infection. The aecia-bearing distal part of the shoot was longer in between 19 % and 37 % of the shoots.

Keywords aecia, *Cronartium flaccidum*, lesion, *Pinus sylvestris*, resin top
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Received 5 October 1999 **Accepted** 24 January 2000

1 Introduction

Cronartium flaccidum (Alb. and Schwein) Winter is among the most destructive pine pathogens in Europe (Gäumann 1959, Wilson and Henderson 1966, Moriondo 1975). The rust is reported to occur commonly on *Pinus sylvestris* L. in southern Scandinavia (Rennerfelt 1943, Roll-Hansen 1973), and sporadically in northern Fennoscandia (Kaitera and Hantula 1998). The dominant rust species in Scandinavia is considered to be the autoecious form of *C. flaccidum*, *Peridermium pini* (Pers.) Lév. (Jørstad 1928, Rennerfelt 1943, Hantula et al. 1998, Kaitera et al. 1999), which causes damage similar to that caused by *C. flaccidum* (Klebahn 1938).

The lesion development, epidemiology and sporulation of *C. flaccidum* is poorly studied and described in Scandinavia. Most reports have referred to *P. pini* (Liro 1908, Jørstad 1928, Rennerfelt 1943). This is mostly due to difficulties in distinguishing *C. flaccidum* from *P. pini* in terms of the disease symptoms and the lack of rapid and reliable identification methods for the two rusts. There are reports dealing with the long-term analysis of rust epidemics in Scots pine stands suffering from *P. pini* (van der Kamp 1970, Greig 1987, Gibbs et al. 1987) but none for stands suffering from *C. flaccidum*.

The aim of this study was to investigate the lesion development of and epidemical patterns caused by *C. flaccidum* in severely damaged pole-stage Scots pines. A further aim was to investigate variation in timing and duration of fruiting and sporulation of the pathogen on infected pines.

2 Material and Methods

The damage pattern in Scots pines was studied annually in late July during the years 1993–97 in an uniform 50 m × 50 m area within a stand of artificially seeded pole-stage pine (Juomukuru 1) severely damaged by rust located in northern Finland (66°17'N, 26°38'E). The site type in the stand was *Hylocomium-Myrtillus* type, the average diameter at the breast-height and height of the trees being 6.2 cm (std = 2.7) and 4.5 m (std = 1.0) measured during another experiment in 1992 (Kaitera, unpublished). The causal rust agent in the stand was earlier identified as *C. flaccidum* (Hantula et al. 1998, Kaitera et al. 1999), the main alternate host to pine for the fungus being *Melampyrum sylvaticum* L. (Kaitera and Hantula 1998).

All trees within the area (106 in number) were checked both at the ground level by observing their lower canopy, and by climbing up the stem using a ladder and checking their upper canopy. The number of lesions in all the trees were counted and active ones were marked on the trees for future monitoring. The length of the lesions (= part of the shoot bearing fruitbodies) bearing fresh aecia (distance between the distal and proximal margins of the shoot bearing aecia), and the age of the shoots bearing the lesion were recorded annually both along the stem and along the branches. At the beginning of the investigation in 1993, the number of old and sporulated lesions in terms of the presence of aecial scars in the shoots and the ages of the shoot bearing the lesion were recorded. The annual growth of the fungus along the shoot (distal and proximal growth) was studied by measuring the distance from the edges of the fresh aecia to whorls and sporulated aecia next to it. In addition, the periods of time from the first sporulation to final sporulation before either killing of the leader above the lesion in terms of browning of the needles and death of buds in the respective shoot, or killing of the fungus in the lesion, while the shoot above the lesion remained alive, were recorded. In practice, the final sporulation occurred always prior to killing of the leader above the lesion. A one-time checking for the occurrence of spermatial fluid from spermogonia on the lesions, was also made in the late July of 1996.

The lengths of the lesions bearing annual aecia were compared between the years. The same applied to the growth of the fungus in distal and proximal directions were done using the TTEST and GLM procedures of SAS (SAS 1989).

3 Results

3.1 Overall Disease Incidence

The percentage of infected trees (at least one lesion per tree) rose from 60.4 % in 1993–94 to 62.3 % in 1995, 66.0 % in 1996, and 67.0 % in 1997. The total number of lesions was 460, giving an average of 4.3 lesions per tree. For infected trees only, the corresponding figure was 6.5 lesions per tree (variation 1–24 lesions per tree). Thirty-seven percent of the infected trees bore only 1–2 lesions, while 25 % bore more than 9 lesions.

3.2 Length and Frequency of Annual Aecia

In 1993, old, sporulated lesions occurred most frequently in shoots formed in the years 1980–

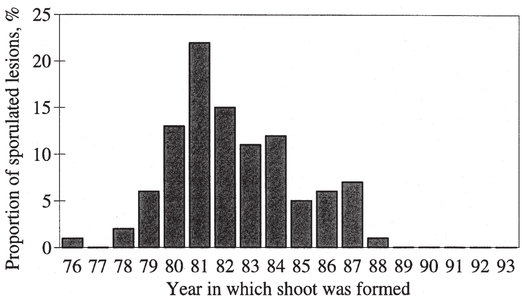

Fig. 1. Variation (%) in the number of shoots bearing sporulated lesions of *Cronartium flaccidum* in shoots formed in 1976–93 in 1993.

84 (Fig. 1), the average length of the sporulated part of lesions being 7.3 cm (Table 1). Ninety percent of these lesions occurred on branches, the rest occurring along the main stem. In the years 1993–97, fresh aecia occurred annually in shoots 3–20 years of age (Table 1). The average age of the shoots bearing fresh aecia was statistically significantly higher in 1997 than in the years 1993–96, and also in 1996 when compared to the years 1993–94 (Tukey's test, data not shown). In the years 1993–97, fresh aecia developed most frequently (between 24 % and 29 %) in shoots formed in the years 1986–87 (in 1993), in the years 1986–88 (15–26 %; in 1994), in the years 1987–88 (22–26 %; in 1995) and in the years 1987–89 (16–22 %; in 1996–97; Fig. 2). Six percent of the lesions bearing fresh aecia occurred along the main stem. The annual average length of the sporulating lesions varied between 3.8 cm and 4.4 cm (Table 1). The length of the lesions bearing aecia was statistically sig-

Table 1. Annual variation in the age and length of shoots bearing aecia.

Year	Average age of shoot, a	Std	Min, a	Max, a	Average length of aecia, cm	Std	Min, cm	Max, cm
1993	7.3	2.39	4	15	3.9	2.81	0.2	13.0
1994	7.9	2.09	3	17	4.1	3.26	0.3	20.0
1995	8.7	2.95	5	18	4.1	4.16	0.1	32.0
1996	9.1	2.94	4	19	3.8	3.16	0.4	21.0
1997	10.0	2.84	5	20	4.4	4.03	0.2	21.0

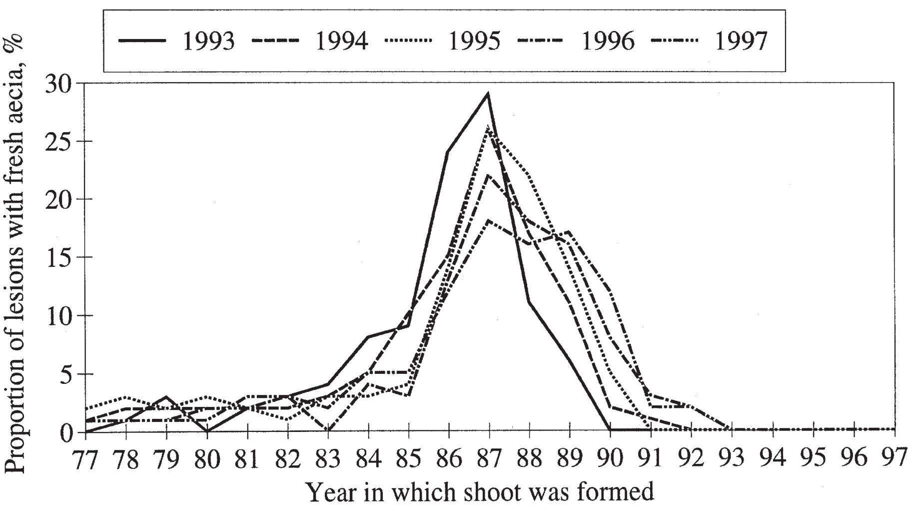

Fig. 2. Annual variation (%) in the number of lesions bearing fresh aecia in shoots formed in 1977–97 in 1993–97.

nificantly greater only between the years 1995 and 1993 (Tukey's test, data not shown). No spermatial fluid was observed on lesions in 1996.

3.3 Age of Branches Bearing Aecia for the First Time

During the years 1993–97, 248 lesions were found which were bearing aecia for the first time. Eighty-three percent of these lesions were produced on 5–10-year-old shoots, while 12 % occurred on shoots more than 10 years old, and only 3 % on shoots less than 5 years old (Fig. 3). The former aecia occurred most frequently (19–22 %) on shoots formed in the years 1987–89. Three percent of these aecia occurred on the main stem.

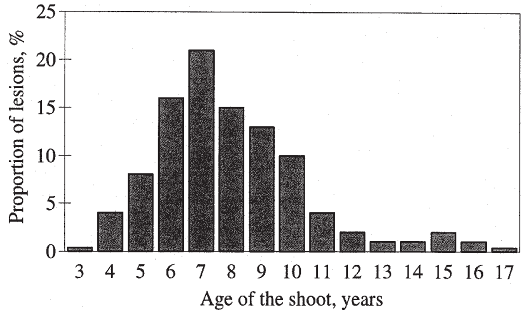

Fig. 3. Variation in the age of the shoots (%) bearing lesions with aecia sporulating for the first time in 1993–97.

3.4 Annual Growth of the Fungus along the Shoot

In 54 % of the lesions, the annual lengths of the lesions bearing fresh aecia were higher in the proximal direction than in the distal direction next to previous year's sporulated aecial scars. In 31 % of the cases, the said length was higher in the distal directions, whereas in 15 % of the cases the length was equal in both distal and proximal direction (Table 2). On the lesions, the average annual growth of the fungus in terms of the presence of fresh aecia was 2.15 cm in the proximal direction (annual variation 1.74–2.71 cm; Table 2), and 1.80 cm in the distal direction (annual variation 1.19–2.88 cm; Table 2). No statistically significant differences occurred in the growth of the fungus along the shoots when combining all the observations (TTEST; $T = 1.36$, $p = 0.175$). Some variation, however, occurred among years, whereas there was statistically significantly higher year-to-year growth of the fungus in the proximal direction than in the distal direction in 1996–97 (TTEST; $T = 2.56$, $p = 0.013$*). Annual growth was at its highest in 1995–96 in both the distal and the proximal direction. No statistically significant year-to-year differences occurred in the annual growth of the fungus in the proximal direction (Tukey's test, data not shown). The growth of the fungus was, however, significantly higher in the distal direction in 1995–96 than in 1996–97, respectively (Tukey's test, data not shown).

Table 2. Average annual growth of *Cronartium flaccidum* in terms of the length of fresh aecia in the proximal and distal directions of infected shoots. Proportion of lesions in which growth is higher in the proximal direction, distal direction and equal in both directions.

Years	Average growth, cm		Percent of lesions, %		
	Proximal	Distal	Proximal > Distal	Proximal < Distal	Proximal = Distal
1993–94	1.74	1.67	51	37	12
1994–95	2.03	2.02	54	35	11
1995–96	2.71	2.88	47	37	16
1996–97	2.35	1.19	59	19	22
Total	2.15	1.80	54	31	15

3.5 Duration of Sporulation

The average duration of aecia production among the lesions that started and finished sporulating during the observation period was 1.73 years. Of the lesions, 51 %, 31 %, 11 % and 6 % sporulated for one, two, three and four years, respectively. In individual years, 17 %, 36 %, 33 % and 49 % of the lesions sporulated for one year when started in the years 1993–96, whereas 34 %, 30 % and 27 % of them sporulated for two years when started in the years 1993–95. When sporulation started in 1993–94, 13 % and 15 % of the lesions sporulated for three years, whereas 13 % of the lesions sporulated for four years when started in 1993. The rest of the lesions (and the leader shoot above them) remained alive and continued to sporulate at the end of the experimental period in 1997, the respective proportions of lesions sporulating for ≥ 5 years (started in 1993), ≥ 4 years (1994), ≥ 3 years (1995) and ≥ 2 years (1996) being 23 %, 18 %, 40 % and 51 %.

As regards the old lesions that had started to sporulate before 1993 and finished sporulating during the experimental period, 24 %, 38 %, 8 % and 16 % of the lesions sporulated for one, two, three and four years. Fourteen percent of these lesions sporulated in the years 1993–97, stayed alive (together with the leader shoot above the lesion) at the end of the experiment, and thus sporulated for ≥ 6 years.

4 Discussion

The results of this study showed that the number of *C. flaccidum* lesions per tree was higher than in similar studies on Scots pine affected by *P. pini* (e.g. van der Kamp 1970). The fact that most of the lesions occurred on a small proportion of the trees has also been reported for *P. pini* on Scots pine (Rennerfelt 1947, van der Kamp 1970, Gibbs et al. 1987), and for other autoecious pine stem rusts (e.g. van der Kamp et al. 1995).

Sporulated *C. flaccidum* lesions were most commonly centred on shoots that were formed during a few years in the early 1980s. In addition, the frequency of fresh lesions was highest in shoots formed during a few years in the late 1980s, after which the number of fresh lesions reduced in shoots formed in the 1990s. In Britain, van der Kamp (1970) showed that the number of *P. pini* infections peaked in a few, close years. Wave years in pine stem rust infections have been reported commonly in North America (Peterson 1971; van der Kamp 1988). Van der Kamp et al. (1995) reported that as high a proportion as 90 % of the damage caused by *Endocronartium harknessii* (J. P. Moore) Hirat. on *Pinus contorta* (Dougl.) originated from one year. Such wave years in infection caused by an autoecious rust do not, however, necessary co-incide with infections by heteroecious rusts (Peterson 1971). In this study, the variation in infections caused by the rust among years was higher compared to corresponding variation caused by related rusts in North America (Peterson 1971; van der Kamp et al. 1995). Reports of similar studies dealing with *C. flaccidum* epidemics and lesion development on Scots pine in Scandinavia are lacking to confirm the generality of the results of this study. Due to lack of meteorological long-term data in the area, the possible effect of precipitation, for example, in infection in epidemical wave years cannot be accurately investigated. The effect of climatic factors on disease development and spread of the disease may be strong, as has been shown for *C. flaccidum* in Italy (Ragazzi 1983), *Cronartium ribicola* Fisch. in North America (Van Arsdel et al. 1956) and for other rusts, e.g. *Melampsora pinitorqua* (Braun) Rostr., in Finland (Kurkela 1973a, b).

In the present study, aecia were produced in 3–20-year-old shoots, the annual average age of the respective shoots being 7–10 years. According to Rennerfelt (1943) and van der Kamp (1970), *P. pini* aecia are observed most frequently in 2–4-year-old pine shoots. In inoculation experiments, several authors have also shown that *P. pini* aecia are formed primarily 2–4 years after infection (e.g. Haack 1914). Gibbs et al. (1987), however, found that 90 % of the active lesions occurred in 3–7-year-old shoots. Rennerfelt (1947) also noted that 30-year-old *P. pini* lesions can readily produce aecia in mature pine trees. As *C. flaccidum* infects pine needles by basidiospores (Klebahn 1924), and the formation of aecia is prolonged by several years in the case of a needle infection by *P. pini* compared to direct shoot infection via wounds (van der Kamp 1970), the frequent production of fresh aecia in relatively old shoots seems reasonable. Earlier, Klingström (1972) succeeded in infecting Scots pine by *P. pini* only when inoculating the youngest needles and shoots but never the older ones. In addition, Ragazzi and Dellavalle Fedi (1992) showed that primary needles are most easily infected by *C. flaccidum* but also the secondary needles can be infected. Nevertheless, thorough studies dealing with *C. flaccidum* infection by basidiospores via needles of different age or wounds in relation to aecia production are lacking. In case the basidiospore infection occurs commonly via secondary needles in old shoots, or the fungus is able to grow through internodes and sporulate far from the primary place of infection without leaving any signs of infection between these places, dating of the actual year of infection becomes difficult. The relatively slow growth rate of the fungus along the shoots and successive fruiting next to previous year's place of fruiting in this study does not, however, support the latter possibility.

In the present study, aecia appeared for the first time in 5–10-year-old shoots in most of the cases, whereas only a few percent of the shoots bearing fresh aecia were less than five years old. Van der Kamp (1970) in Britain showed that all the *P. pini* aecia that sporulated for the first time appeared in 2–4-year-old pine shoots. Gibbs et al. (1987) also in Britain reported of a similar case, the proportion of 5-year-old shoots bearing aecia being less than 20 %. The latter report is relatively comparable to the present report, whereas the corresponding rust agent was also able to infect alternate hosts to pine to some degree (Gibbs et al. 1988). The delay in *C. flaccidum* aecia production (compared to that of *P. pini*) may also be explained by the inefficiency of the fungus to fulfill its life cycle. This may be caused by insufficient spermatization due to low frequency of spermogonia (as suggested by the results of this study), or poor ability of insect vectors to transmit spermatia among lesions.

The annual growth of *C. flaccidum* by means of the length of fresh aecia was insignificantly higher in the present study in the proximal direction compared to the distal direction with some year-to-year variation. Earlier, Olembo (1971) reported of *P. pini* growing faster in the proximal direction in terms of stem swelling. Hertz (1930) also reported (without identifying the rust agent) that pine stem rust grows most rapidly vertically rather than radially or circularly along the stem. Gibbs et al. (1987) found similar year-to-year and site-to-site variation between annual distal and proximal growths of *P. pini* on Scots pine, as was the case in this study. In general, the annual growth of *C. flaccidum* in this study was about the same as that of *P. pini* in Scotland (van der Kamp 1970), but lower as that of *P. pini* in Thetford, southern England (Gibbs et al. 1987).

In the present study, most of the lesions sporulated for only 1–2 years before killing the shoot above the infection point and finishing of sporulation. A small number of lesions, however, sporulated for ≥ 6 years. This may be an indication of variation in pathogenicity of *C. flaccidum*, or resistance of the host tree. No similar studies are available to confirm these results.

Acknowledgements

Forest technician Pekka Närhi and Ossi Huusko, B.Sc (For.), helped in the field work. Tarmo Aalto, B.Sc (For.), drew the graphs for the manuscript. Erkki Pekkinen, M.Sc. (For.), checked the English. Professor Timo Kurkela gave valuable comments on the manuscript.

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