forests

Article

Synthesis and New Observations on Needle Pathogens of Larch in Northern Finland

Risto Jalkanen

Received: 16 November 2015; Accepted: 13 January 2016; Published: 18 January 2016
Academic Editors: Jan Stenlid, Jonas Oliva and Audrius Menkis

Natural Resources Institute Finland, Rovaniemi Research Unit, Rovaniemi 96300, Finland; risto.jalkanen@luke.fi; Tel.: +358-50-391-4430

Abstract: Needle pathogens of larch (*Larix* spp.) in the Nordic countries are under-studied. Their incidence in Finland tends to be low and local, and this may be a function of enemy release, since species of larch were introduced to the region. Here, the ecology and incidence of larch needle pathogens and the abiotic factors that also affect larch in northern Finland are reviewed. Field observations and related laboratory analyses during the past 35 years have mainly been obtained near the Kivalo Research Area within the Arctic Circle, Finnish Lapland. The relatively recent introduction of *Hypodermella laricis* is a primary focus. This pathogen is not only new to Nordic countries, but can cause severe outbreaks, defoliation and crown-thinning in the canopies of all ages of most planted larch species worldwide. Symptoms of *H. laricis* clearly differ from those of *Mycosphaerella laricina*; the latter has affected *Larix sibirica* at high latitudes for decades. The effects of *Meria laricis*, *Lophodermium laricinum*, various rust fungi, and wind and frost are also discussed.

Keywords: Larix; Hypodermella laricis; Mycosphaerella laricina; Melampsora; Melampsoridium; rusts; alternate hosts; Betula; Salix; Alnus

1. Introduction

Native larch (*Larix* spp.) grows largely in cool zones of the Northern hemisphere. Its environments are mainly mixed or pure boreal forests, where it often forms the northern or alpine conifer tree line. About 10 different larch species of this highly hybridizing genus have been recognized [1]. Although none of these species is native to Finland, larch is known to have grown during the more continental climate of the Eemian interglacial period about 130,000–115,000 years ago in the territory of current Finland [2]. Thus, the question whether the large Eemian sub-fossil larch log excavated in northern Finland justifies the naming of larch as a native species is mainly academic. Nevertheless, the recent larch history in traditional Finnish territory is short and consists of roughly one to two generations only; the famous seed source of Siberian larch (*L. sibirica* Ledeb.) was introduced to Raivola, on the Carelian Isthmus in 1738 [3]. Since then, and mainly in the twentieth century, most larch species and subspecies, as well as many hybrids, have been introduced and tested for their growth and survival in Finland [4]. Currently, there are over 20,000 ha larch plantations in Finland [5]. In northern Finland, where the Raivola seed source of Siberian larch is superior in growth and survival, three other larch species can form proper stands: European (*L. decidua* Mill.), Dahurian (*L. gmelini* (Rupr.) Litv.), and tamarack larch (*L. laricina* (Dur.) K. Koch).

Larix is commonly considered to be a tolerant genus against pests, diseases and abiotic factors, especially in Nordic environments, where larch has a short history as an introduced genus and, thus, a rather restricted co-evolution with pests and pathogens. Wide heartwood, thick latewood rings and high contents of secondary metabolites in the stem and deciduous foliage are considered reasons for the high resistance of larch trees. Furthermore, local seedling production supports the larch health status. However, larch in Finland is not free of pests and pathogens; typically, a great majority of these pests are monophagous and occur only in larch [6]. In Finland, the main pathogenic problem, especially in European larch, is European larch canker caused by *Lachnellula willkommii* (Hart.) Dennis [1,4]; this fungus infects shoots and causes cankers in the stem and shoots. Larch foliage diseases have received little attention in Finland.

Recently, a needle-inhabiting ascomycete, *Hypodermella laricis* Tub., which is new to the whole of Fennoscandia, was recorded in northern Finland [7]. Because another needle pathogen, *Mycosphaerella laricina* (R. Hartig) Miq., has occurred for decades in northern Finland, this presented a good opportunity to provide an update on the situation concerning fungal pathogens and common abiotic factors among larch needles in northern Finland.

2. Experimental Section

The data consisted mainly of observations in field campaigns in larch stands of various ages, and of laboratory analyses performed during the last 35 years. The main target area was the Kivalo Research Forest (latitude 66.29°–66.47°; longitude 26.58°–26.84°) of the Finnish Forest Research Institute (Metla) in the Arctic Circle in Rovaniemi, northern Finland. The oldest stands of Siberian and European larch were established in 1929 and 1949, respectively [4] and the youngest Siberian ones in 2006 [8].

3. Results and Discussion

3.1. *Hypodermella laricis* Tub.

Larch needle blight caused by *Hypodermella laricis* was first described in Central Europe on European larch 120 years ago [9] and is now common at high elevations of the Alpine region above 1000 m [10–13], and on larch in Siberia [14]. It is native to North America and was also recorded on western larch (*L. occidentalis* Nutt.) in Idaho, USA, in 1911 [15] and, subsequently, widely on western larch in British Columbia, and on tamarack in Ontario, Canada and in the eastern United States [16]. Nowadays, this larch needle blight occurs in a wide range of larch species that grow natively or have been introduced to the Northern hemisphere.

The first record of *H. laricis* in northern Europe was in 2007, when larch needle blight broke out in a 60-year-old European larch stand (est. 1949) in Kivalo Research Area [7]. In subsequent years, it spread to most stands of the Kivalo area, most of which consisted of Siberian larch (Figure 1); Dahurian larch also became infected, but tamarack has remained healthy, at least to date. The pathogen has infected needles annually since 2007, although the strength of the outbreak varies greatly from year to year. It is notable that the disease occurs only in the Kivalo area in the Arctic Circle, although over 20,000 ha of planted larch exist throughout Finland [5]. All sites where *H. laricis* has been recorded are located at an altitude of 220–350 m a.s.l. (above sea level), whereas most Finnish plantations are located far below 200 m. The Kivalo hill range could be considered to resemble the Alpine region, where sites above 1000 m a.s.l. favor *H. laricis* [11]; the theoretical tree line in Kivalo would be present at 450–500 m a.s.l. if the "high" hill were to exist. Furthermore, due to land heaving, all sites currently locating above 200 m a.s.l. in Kivalo are supra-aquatic, *i.e.*, they were never covered by the Baltic Ice Lake in the early Holocene. Thus, soils at higher altitudes have stayed rich in nutrients, which might have caused larch to become susceptible to *H. laricis*. The Alpine area was probably the source of the outbreak in Kivalo, but the reason why only at this site remains unclear. One plausible hypothesis is that the late spring in the Alps and early spring in the Arctic Circle, together with persistent winds from the South and high humidity, coincided with the foliage flush.

Figure 1. Massive 2011 outbreak of *Hypodermella laricis* in the Siberian larch stand planted in 1929, Kivalo Research Forest, 29 June 2011.

Vilcan *et al.* [13] have reviewed and generalized the principles of the life cycle and etiology of *H. laricis* in short: "Infection by spores occurs in early spring as soon as the leaves emerge, but there is no evidence that hyphae invade the dwarf shoots. The fungus disrupts the normal abscission mechanism, and the fructifications and spores of *H. laricis* develop on the leaves that remain attached to the dwarf shoots. Fruiting bodies (hysterothecia) form soon after the needles are killed and turn brown, appearing as elliptical black spots. The time of precipitation is a decisive factor in the initiation of this disease; infection occurs only when precipitation coincides with the emergence of young leaves. However, vulnerability to infection disappears once the needles become mature."

Some points in the above description deserve comment, although the appearance of symptoms is similar (Figure 2). First of all, the growing season in the North is short. This means that needle flush occurs on average at the start of June, resulting in the appearance of symptoms during the first and second week of June. Among the initial symptoms, grayish green needles turn light brown within a week, when a needle-long black line of fruiting-body structures appears in the adaxial midrib region. The longitudinal black line is more or less continuous at this time but subsequently becomes much compartmented during the season. At the beginning of the development, asexual conidiomata are formed in the midrib region along the entire length of the needle (Figure 2b) and, later, elliptical ascomata (Figure 2c) arise and the line of continuity disappears during the summer. The needle surface around the black fruiting bodies is light-brown or slightly reddish brown. From a distance, the canopy color is more strongly reddish brown, which is a characteristic symptom of the disease.

(**a**)

(**b**)

(**c**)

Figure 2. Symptoms of *Hypodermella laricis* in the Kivalo Research Forest. (**a**) Newly infected reddish-brown needles are already drooping with visibly developing fruiting bodies; the spur shoot is recovering with a new set of needles; the previous year's infection has resulted in needles that direct downwards in one spur shoot and the death of two spur shoots next to it; Siberian larch, 12 July 2011; (**b**) Conidiomata of *Leptothyrella laricis*, on a Siberian larch needle primarily infected by *Hypodermella laricis*, 18 June 2011; (**c**) Open hysterothecia of *Hypodermella laricis* on European larch, one year after infection, 22 June 2014.

Dearness [17] has described *Leptothyrella laricis* Dearn. as the asexual state of *H. laricis* var. *octospora* Dearn., the eight-spore variety of *H. laricis*. Furthermore, Funk [18] and Minter [14] mention that *L. laricis* is an anamorph to *H. laricis*. However, most authors do not mention the asexual state in connection with describing field observations at all. The anamorphic phase appears soon after infection in relation to the initial symptoms and lasts a short period, to be replaced by the formation of clearly more visible and larger ascomata. Conidial structures are inconspicuous and the spores are exceptionally small (3–5.6 × 1.2–1.9 μm) [19], and the nature and functional role of these structures are unknown.

Ascospores germinate on and penetrate the meristematic tissue at the needle base. Cohen [20] described how the abscission zone is formed in healthy and diseased larch needles and found that the infection triggers *H. laricis* to form a typical black band at the base of each diseased needle very early after infection. This is most probably related to the disruption of the normal abscission mechanism, which keeps the needles attached for the duration of the life cycle, and often even much longer, according to past outbreaks. *Hypodermella laricis* has been reported to have a one-year life cycle (e.g., [20]). Hysterothecia develop in the needles that hang from the spur shoots, *i.e.*, short or dwarf shoots. However, in Kivalo Research Forest, most infected needles stay attached to their spur shoots for several years. Additionally, hysterothecia on some needles remained unopened after the third or even fourth year of infection, thus having ascospores one to two years longer than normal. Although most authors state that *H. laricis* has a life-cycle that lasts only one year, Darker [21] has reported that the life cycle of *H. laricis* on tamarack from initial infection to sporulation lasts for at least two years, similar to Kivalo observations. A delay in sporulation might have evolved because the development of the spur needles after the flush to maturation, *i.e.*, the time during which they are susceptible, is rather short. Furthermore, the relative humidity in Kivalo at this time of year is low, which does not favor infection. Notably, a related species that causes needle cast in Norway spruce (*Picea abies* (L.) H. Karst.), *Lirula macrospora* (Hart.) Dark., which has a two-year life cycle [22], also appears to have a partial delay of several years in the opening of the hysterothecia at high latitudes.

As needles are infected via the meristematic tissue at their base, emerging needles of the spur shoots mainly become infected. Spur shoots display many variations in needle death; it is common that all needles die, but in the least severe cases, only a single needle is infected. The youngest spur shoots, initiated in the previous year, recover by producing new needles in the same year of infection (Figure 2a), thus showing clear greening towards the end of the summer. However, older spur shoots die if needles of the spur shoots are infected in two consecutive years [20], causing severe and permanent crown thinning, especially in the canopy of European larch.

It has been seldom mentioned in the literature that needles on the long shoot (juvenile growth) can also become infected. In Kivalo, where juvenile shoots became strongly infected in 2011, fruiting-body structures also formed on their needles. This raises the question whether the source of infection was the ascospores of late-opened hysterothecia or spores of the anamorph, which sporulated in the infected needles of the spur shoots at the time of juvenile growth. If the "conidial" particles are spermatia rather than infectious spores, the source of infection was ascospores of *H. laricis*. Infections in long shoots appear to accelerate crown thinning via shoot-tip deaths.

3.2. *Mycosphaerella laricina* (R. Hartig) Miq.

A larch needle cast fungus, *Mycosphaerella laricina*, was described in Europe more than 100 years ago [23]. This species most probably appeared on European larch in the United States in the early 1970s, with the first record being from 1980 [24].

The history of *M. laricina* in Kivalo Research Area is unknown. The first larches were planted in the area in 1929 and the first records of the disease date from the early 1980s, when the fungus was abundantly fruiting on needles of the lower canopy of trees in a 5–6-m tall Siberian larch plantation in the Arctic Circle. Soon, it appeared in dense plantations throughout Lapland, and nowadays it is continuously present in the Kivalo Research Forest. The disease symptoms resemble autumn colors; the needles turn red, brown and yellow in patches and in longer bands, mixed with still green parts and they remain stiff until they are cast. The discoloration and formation of asexual fruiting bodies start from needle tips basipetally (Figure 3a,b). The disease is most severe in the lowest part of the canopy.

The disease appears to infect needles only, thus being a real needle-cast disease. However, as discoloration appears as early as in July in some years, weakened lower branches might undergo secondary damage; dead branches contribute to crown-thinning of the lower canopy (Figure 3c). *Mycosphaerella laricina* is known to cause a serious loss of productivity [25], which is also a problem in some forest nurseries [26].

(**a**)

(**b**)

(**c**)

Figure 3. (**a**) Symptoms of *Mycosphaerella laricina* on Siberian larch needles in Kivalo Research Forest, Rovaniemi, 11 August, 2011; (**b**) Asexual state of *Mycosphaerella laricina* on Siberian larch needles in Maaninkavaara, Kuusamo, 23 August 2013; (**c**) Crown-thinning in the lower canopy of a Siberian larch caused by severe subsequent infections of *Mycosphaerella laricina* in Kivalo Research Forest, Rovaniemi, 11 August 2011.

In Kivalo, autumn discoloration by *M. laricina* occurs annually, although to a lesser extent and later in the season in dry than wet summers. There are no reports on the life cycle of this fungus in the northern larch forests. Maresi *et al.* [12] have suggested that the widespread outbreak in August 1999 was due to ascospores that formed in fallen needles. Palmer *et al.* [27] have shown that ascospores predominate in May–July and conidia in August–September. In the area studied here, the role of the sexual state in the infection process is unknown.

3.3. *Meria laricis* Vuill.

A larch needle cast fungus, the hyphomycete *Meria laricis*, was described in France in 1896 [28] and has been known in North America since the 1940s [16]. It is also common on introduced larches in New Zealand [29]. Although the fungus infects needles on trees of all sizes, this species is found mainly on seedlings and saplings. Even if *M. laricis* affects seedlings in tree nurseries, it can cause severe outbreaks in larger stands [12]. In Europe and the United States, the pathogen has been controlled successfully with fungicides [30,31]. In Finland, *M. laricis* might have been recorded only once on Siberian larch seedlings in a tree nursery [32,33]; however, it is highly uncertain whether this pathogen has affected any of the Finnish forest nurseries [34]. No records of *M. laricis* exist from trees in northern Finland. Funk [18] has reported that *M. laricis* also infects Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco). However, this might be based on mistaken identity, because the related and common species on Douglas fir needles, *Meria parkeri* Sherwood, J.K. Stone & G.C. Carroll, had not yet been described at the time of Funk's writing.

Meria laricis overwinters in fallen needles. Conidial production begins at the time of needle flush and continues for as long as the humidity is suitable. In a wet summer, sporulation can occur throughout the entire growing season. Therefore, symptoms can appear during a wide range of dates during the summer. Infection is common in nursery beds, where the infection source is next to the new needles and when humidity is high. Infection points initially turn yellow and then form broad red-brown bands, which are the most visible symptoms of the disease. The conidia, which are invisible and ooze out through whitish stomata, are formed on the under (abaxial) side of the needles. Needles are shed relatively rapidly before the end of the growing season. Only immature needles are susceptible, meaning that later in the season, only needles of the juvenile long shoots and growing current-year seedlings may become infected. The sexual state of *M. laricis* is unknown, but Gernandt *et al.* [35] suggest that it belongs to the genus *Rhabdocline*.

3.4. *Other Needle Cast Fungi*

Lophodermium laricinum Duby, described by Duby in 1861 [36], is often mentioned as one of the pathogens that infects larch needles [11,13,19]. A typical characteristic of *Lophodermium* species is that they fruit on fallen needles [37] and infrequently cause black lines across the needles [38]. Several authors suggest that *L. laricinum* causes premature needle-shed, and is thus a pathogen of green needles [21,22,37] on a wide variety of larch species [14]. The author detected *Lophodermium*-type fruiting bodies in the needle litter, which resembled those of *L. pinastri* (Schrad.) Chev., suggesting that *Lophodermium* sp. is present at least as a saprophyte at high latitudes in Lapland (Figure 4). Similarly to von Tubeuf [39], the author was unable to find evidence of its pathogenicity in the field. Minter [40] even suspects that *L. laricinum* and *L. pinastri* are the same species.

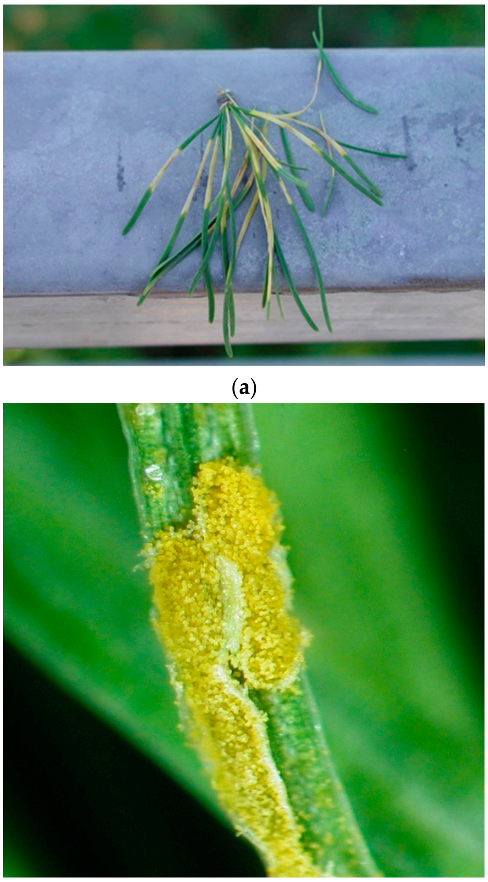
Figure 4. Abundant *Lophodermium* sp. on previous-year needle litter of Siberian larch in the Kivalo Research Forest, Rovaniemi, 19 June 2015. Some needles are full of fruiting bodies of *Mycosphaerella laricina*.

Sarcotrochila alpina (Fuckel) Höhn., which has been recorded on European larch [41], also fruits on attached needles of several North American larch species [37]; this species has not been recorded in the Kivalo larch forests.

In addition, one unnamed species has been recorded to infect and sporulate in attached larch needles.

3.5. Rusts

Several rust species known to infect larch as an alternate host, occur at northern latitudes on broadleaved tree species such as native birches (*Betula* sp.), willows (*Salix* sp.), gray alder (*Alnus incana* L.), aspen (*Populus tremula* L.), and introduced poplars (*Populus* sp.). Pathogenic *Melampsora* and *Melampsoridium* species infect larch needles in the high season of the summer, when the foliage just reaches maturity. Presumably, all these species can form aecia with aeciospores on green larch needles. However, their identification at the species level, based on visual observation and measurements of aecia and aeciospores, appears to be rather uncertain. The common rust species known from Lapland belong to the Caeoma I aecial type [42] (Figure 5a,b). Nevertheless, needle rusts on larch appear to infect only scattered needles, and neither massive outbreaks nor premature needle shed due to rust infection has been observed in northern Finland.



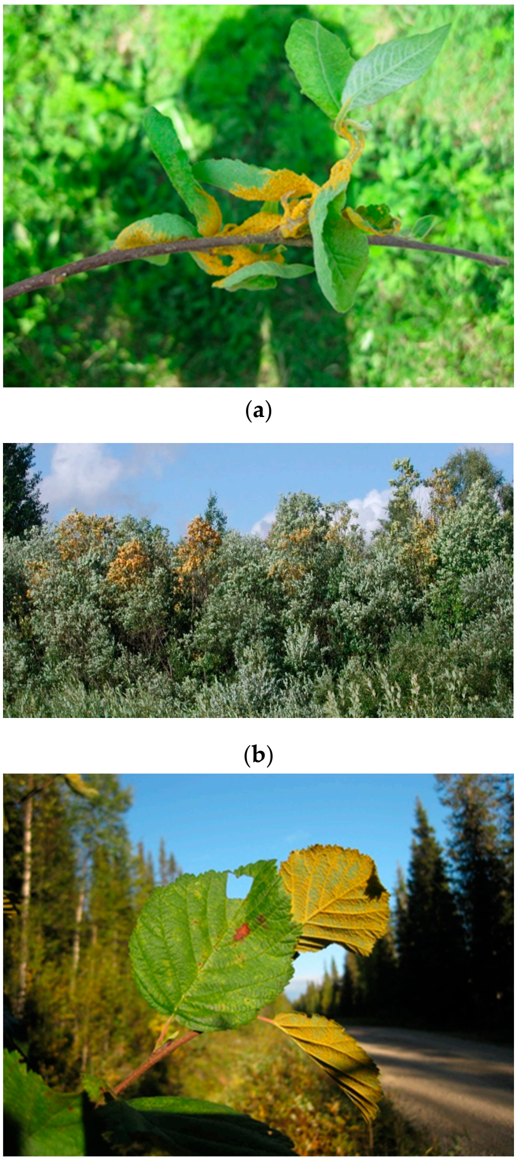
(**a**)

(**b**)

Figure 5. (**a**). Exceptionally heavy rust infection on a spur shoot of a hybrid larch sapling, Rovaniemi, 2 July 2006; (**b**) The aecial state of an unspecified rust species on a Siberian larch needle, Kivalo Research Area, 24 June 2007.

In Finland, at least seven rust species with an aecial state on larch needles occur on broadleaved trees: *Melampsora caprearum* Thüm., *M. laricis-epitea* Kleb., and *M. laricis-pentandrae* Kleb. on willows, *M. laricis-tremulae* Kleb. on aspen, and *M. laricis-populina* Kleb. on poplars [43–45]. Furthermore, one *Melampsoridium* species is known on birches [46] and another on alders [47].

Several *Melampsora* species are extremely common in Lapland, almost annually. Most likely *M. caprearum* on willows and especially on *Salix caprea* L., effectively destroys shoot tips and even forms cankers on the shoot stem, resulting in weakened survival during the winter. As a special case in northern Finland, *M. caprearum* populations on *S. caprea* appear to be systemic; massive sporulation begins in shoots and tiny leaves as soon as buds start to unfold. Due to sporulation, trees can appear as if they are blooming in late May (Figure 6a). This always leads to direct shoot death and after several years, to the death of the canopy. Despite only fewer than 10 infested *S. caprea* trees, this phenomenon raises the need to study whether an alternating rust species has evolved to become a non-alternating one from willow/larch to willow only, respectively.



(**a**)

(**b**)

(**c**)

Figure 6. Rust on broadleaved trees. (**a**) Systemic-like infection and sporulation of *Melampsora* sp. on *Salix caprea*, Rovaniemi, 2 June 2009; (**b**) *Salix pentandra* trees or bushes can easily be detected when heavily infected by *Melampsora laricis-pentandrae*, Tervola, 5 August 2005; (**c**) A shoot of *Alnus incana* infected by *Melampsoridium hiratsukanum* in Kivalo Research Forest, Rovaniemi, 2 September 2013.

Already in the 1980s, *M. laricis-pentandrae* became an annual phenomenon on *S. pentandra* L., a common species in southern Lapland. Heavily infected bay-leaf willows can be seen from July onwards every summer (Figure 6b), and the few occasionally planted poplars, mainly balsam and black poplars, become heavily infested by *M. laricis-populina* from late July, irrespective of the summer climatic conditions. Heavy infections have occurred in the last 10–15 years.

The most common rust fungus that can alternate between birch and larch is *Melampsoridium betulinum* (Pers.) Kleb., the basidiomycete causing birch rust disease [48]. During a wet summer, outbreaks of this rust occur on most birch species, which are increasingly frequent on silver birch due to a different race of the pathogen [46]. The disease is most severe in pubescent birch, which appears naturally and abundantly in every stand in Lapland. The pathogen has the uredinial state on leaves still attached to trees, and the telial state on fallen leaves. There should be no obstacle to a large outbreak on larch next season, when teliospores generate basidiospores. However, hardly any traces of infection are visible in needles of adjacent larches, although outbreaks have appeared repeatedly on birch. This suggests that larch is not necessary for the repeated outbreaks of birch rust from year to year.

Melampsoridium hiratsukanum S. Ito ex Hirats. f. was reported on alder for the first time in southern Finland in 1997 [47] and in the southern part of northern Finland in 2003 [49], and finally on the hills of the Kivalo Research Forest in 2013 (Figure 6c); it was also common on grey alder (*Alnus incana* L.) in 2015. However, although *M. hiratsukanum* can sporulate on larch needles, no signs indicate that rusts on larch needles have become more common in the Kivalo Research Forest or elsewhere in the northern larch forests. The Dahurian larch, which is necessary for a new long-term settlement of *M. hiratsukanum* [50], is present in Kivalo and might contribute to the persistence of *M. hiratsukanum* in the area.

3.6. Wind and Frost

It is very evident that needles of younger larches or lower branches of large trees are susceptible to strong northerly or generally continuous winds, especially at near or below-freezing temperatures (Figure 7). Although needles are more susceptible in the early part of the season, they can also be damaged later in the season. If the damage occurs early in the season, trees can produce a new set of needles from spur shoots later in the season. Typical wind and/or low temperature damage seldom has any particular pattern, unless canopies are injured on one side. Nevertheless, needles become reddish brown and resemble the reaction after a fungal infection. Needles affected by abiotic factors shed easily, indicating no pathogenic infections.

Figure 7. Juvenile needles of Siberian larch that have suffered from a cold wind. This type of abiotic injury is often only on one side of the canopy or even on a small part of it. Kivalo Research Area, 2 July 2006.

If a frost occurs so late in the season that long shoots have started to develop, they are more vulnerable than needles of spur shoots to injury by low temperature. Because larches and especially saplings appear to grow for longer than other conifers in the Research Forest, most damage due to low temperature is caused by early frost, *i.e.*, an effect of early autumn cold on less hardy shoot tips.

4. Conclusions

Although over 20,000 ha of mainly Siberian larch have been planted in Finland, there has been surprisingly little research performed on pathogens that cause foliage, shoot and stem diseases in the species of the genus; knowledge is scarce and the references are scattered and derive mainly from temporary field observations. More research is required both among homophagous needle and shoot pathogens and host-alternating rust fungi. There is a lack of knowledge on the life cycle and pathogenicity, as well as factors that affect the host susceptibility of all needle cast and needle blight fungi. It is desirable to understand the threats that result from the changing environment before all the pathogens break out at the same time (see [12]). We need a better understanding concerning the absence of outbreaks by rust fungi on larch needles, although these are common on broadleaved trees adjacent to larch, which is the obligate alternate host. Although modern techniques help us to determine the aecial states of needles at the species level, they might not reveal the huge difference in disease incidence between the two host species, and the role of larch in the life cycle of rust fungi is unclear.

Acknowledgments: The author is grateful to the Hyypiökivalon Pyyntömiehet hunting club for the use of the Mustaoja log cabin during field campaigns. Furthermore, the Finnish Forest Research Institute (Metla) that was merged with the Natural Resources Institute Finland on 1 January 2015 is acknowledged for the positive support in field surveys of pathogens and pests in Finnish forests.

Author Contributions: The author was solely responsible for the sampling and analysis of the material, and the manuscript preparation.

Conflicts of Interest: The author declares no conflict of interest.

References

1. Sarvas, R. *Havupuut*, 1st ed.; WSOY: Porvoo, Finland, 1964; p. 518. (In Finnish)
2. Mäkinen, K. Tiedonanto Vuotson interglasiaalisesta lehtikuusen rungosta. Summary: Report on interglacial *Larix* trunk at Vuotso, Northern Finland. *Geologi* **1982**, *34*, 183–185. (In Finnish)
3. Ilvessalo, L. Raivolan lehtikuusimetsä. Referat: Der Lärchenwald bei Raivola. *Comm. Inst. For. Fenn.* **1923**, *5*, 104. (In Finnish)
4. Lähde, E.; Werren, M.; Etholén, K.; Silander, V. Ulkomaisten havupuulajien varttuneista viljelmistä Suomessa. Summary: Older forest trials of exotic conifer species in Finland. *Comm. Inst. For. Fenn.* **1984**, *125*, 87. (In Finnish)
5. Silander, V.; Lehtonen, J.; Nikkanen, T. Ulkomaisten havupuulajien menestyminen Etelä-Suomessa. Summary: Performance of exotic conifers in Southern Finland. *Metsäntutk. Tied. Finn. For. Res. Inst. Res. Pap.* **2000**, *787*, 127. (In Finnish).
6. Siitonen, J. Lehtikuusen hyönteistuholaiset Suomessa. *Metsäntutkimuslaitoksen Tied.* **1993**, *464*, 71–78. (In Finnish)
7. Jalkanen, R. Lehtikuusella uusi sienitauti. *Metsälehti* **2013**, *11*, 27. (In Finnish)
8. Lukkarinen, A.; Ruotsalainen, S.; Nikkanen, T.; Peltola, H. Survival, height growth and damages of Siberian (*Larix sibirica* Ledeb.) and Dahurian (*Larix gmelinii* Rupr.) larch provenances in field trials located in southern and northern Finland. *Silva Fenn.* **2010**, *44*, 727–747. [CrossRef]
9. Von Tubeuf, K. *Hypodermella laricis* Tubeuf. *Bot. Zentralbl.* **1895**, *61*, 49. (In German)
10. Donaubauer, E. Schwere Schäden an Lärche in Nieder-und Oberösterreich. *Forstsch. Aktuell* **1992**, *9*, 1–4. (In German).
11. Cech, T.L. Nadelschütten der Lärche. *Forstsch. Aktuell* **2004**, *32*, 11–13. (In German)
12. Maresi, G.; Capretti, P.; Ambrosi, P.; Minerbi, S. Larch crown diseases in Trentino and South Tyrol. *J. For. Sci.* **2004**, *50*, 313–318.
13. Vilcan, A.; Tăut, I.; Holonec, L.; Mihalte, L.; Sestras, R. The variability of different larch clone provenances on the response to the attack by its main pests and fungal diseases. *Trees* **2013**, *27*, 697–705. [CrossRef]

14. Minter, D.W. Hypodermella laricis. *CMI Descr. Pathog. Fungi Bact.* **1988**, *943*, 1–2.
15. Dearness, J. New and noteworthy fungi—IV. Discomycetes including Phacidiaceae and Hypodermataceae. *Mycologia* **1926**, *18*, 236–255. [CrossRef]
16. Garbutt, R. Foliage diseases in Western Larch in British Columbia. *For. Pest Leaflet* **1996**, *71*, 4.
17. Dearness, J. New and noteworthy fungi—V. Deuteromycetes. *Mycologia* **1928**, *20*, 235–246. [CrossRef]
18. Funk, A. *Foliar Fungi of Western Trees*; Canadian Forest Service, Pacific Forest Research Centre: Victoria, BC, Canada, 1985; Volume BC-X-265, p. 159.
19. Ogris, N. Na Jureževi planini se je pojavil ožig macesnovih iglic, ki ga povzroča gliva *Hypodermella laricis*. *Novice Varstva Gozdov* **2013**, *6*, 3–4. (In Slovenian)
20. Cohen, L.I. The pathology of *Hypodermella laricis* on larch, *Larix occidentalis*. *Am. J. Bot.* **1967**, *54*, 118–124. [CrossRef]
21. Darker, G.D. The Hypodermataceae of conifers. *Contrib. Arnold Arbor. Harvard Univ.* **1932**, *1*, 131.
22. Kujala, V. Über die Kleinpilze der Koniferen in Finnland. *Comm. Inst. For. Fenn.* **1950**, *38*, 121. (In German)
23. Hartig, R. Der Nadelschüttepilz der Lärche, *Sphaerella laricina* n. sp. *Forstl. Naturw. Z.* **1895**, *4*, 445–457. (In German)
24. Patton, R.F.; Spear, R.N. Needle cast of European larch caused by *Mycosphaerella laricinia* in Wisconsin and Iowa. *Plant Dis.* **1983**, *67*, 1149–1153. [CrossRef]
25. Ostry, M.E.; Pijut, P.M.; Skilling, D.D. Screening larch *in vitro* for resistance to *Mycosphaerella laricina*. *Plant Dis.* **1991**, *75*, 1222–1224. [CrossRef]
26. Sokolova, E.S.; Golynsky, A.A.; Gordienko, P.V. Premature yellowing and needle-shedding disease of larch. *Zashchita Karantin Rastenii* **2011**, *2*, 47–48.
27. Palmer, M.R.; Ostry, M.E.; Robbins, K.; Nicolls, T.H. Occurrence and development of *Mycosphaerella laricina* on larch in the North Central United States. *Plant Dis.* **1986**, *70*, 921–923. [CrossRef]
28. Vuillemin, P. Les Hypostomacées, nouvelle famille des Champignons para sites. *Comptes Rendu Hebdomadaire Sci. l'Académie Sci. Paris* **1896**, *122*, 546. (In French).
29. Ridley, G.S.; Dick, M.A. An Introduction to the diseases of forest and amenity trees in New Zealand. *For. Res. Bull.* **2001**, *220*, 110.
30. Boudier, B. An attempt to control the drying-out of European larch (*Larix decidua*) needles caused by *Meria laricis* in the nursery. *Rev. For. Franc.* **1981**, *33*, 394–399. [CrossRef]
31. Cooley, S. *Meria Laricis: Fungicide Control and Outplanting Survival of Infected Seedlings*; USDA Forest Service: Portland, OR, USA, 1981.
32. Kurkela, T. Lehtikuusen neulaskaristeet. *Meria laricis* ja *Mycosphaerella laricina*. In *Taimituho-opas*, 3rd ed.; Poteri, M., Ed.; Finnish Forest Research Institute: Suonenjoki, Finland, 2008; p. 100. (In Finnish)
33. Lilja, A.; Poteri, M.; Petäistö, R.-L.; Rikala, R.; Kurkela, T.; Kasanen, R. Fungal diseases in forest nurseries in Finland. *Silva Fenn.* **2010**, *44*, 525–545. [CrossRef]
34. Lilja, A.; Himanen, K.; Poimala, A.; Poteri, M. Metsäpuiden taimituotantoa ja joulupuiden kasvatusta uhkaavat taudit. *Metsät. Aikak.* **2013**, *4*, 647–674. (In Finnish)
35. Gernandt, D.S.; Camacho, F.J.; Stone, J.K. *Meria laricis*, an anamorph of *Rhabdocline*. *Mycologia* **1997**, *89*, 735–744. [CrossRef]
36. Duby, J.E. Rapport sur les travaux de la société de physique de Genève et d'histoire naturelle de Genève de Juillet 1860 à Juni 1861. *Mém. Soc. Phys. d'Hist. Nat.* **1861**, *16*, 58. (In French)
37. Ziller, W.G. *Sarcotrochila alpina* and *Lophodermium laricinum* causing larch needle blight in North America. *Plant Dis. Rep.* **1969**, *53*, 237–239.
38. Luo, J.-T.; Lin, Y.-R.; Shi, G.-K.; Hou, C.-L. *Lophodermium* on needles of conifers from Yunnan Province, China. *Mycol. Progr.* **2010**, *9*, 235–244. [CrossRef]
39. Von Tubeuf, K. Pflanzenkrankheiten durch kryptogame Parasiten verursacht; Eine Einführung in das Studium der parasitären Pilze, Schleimpilze, Spaltpilze und Algen. In *Zugleich eine Anleitung zur Bekämpfung von Krankheiten der Kulturpflanzen*; Springer: Berlin, Germany, 1895; p. 599. (In German)
40. Minter, D.W. The *Rhytismatales* on conifers from Europe. In Shoot and Foliage Diseases in Forest Trees, Proceedings of a Joint Meeting of the Working Parties: Canker and Shoot Blight of Conifers, and Foliage Diseases, Vallombroza, Italy, 6–11 June 1994; Capretti, P., Heiniger, U., Eds.; Università degli Studi di Firenze: Firenze, Italy, 1995; pp. 65–84.

41. Von Höhnel, F. Fragmente zur Mycologie 1010. *Sitzher. Acad. Wiss. Wien, Math. Naturw. Kl. I* **1917**, *126*, 305–314. (In German)
42. Sato, T.; Sato, S. Morphology of aecia of the rust fungi. *Trans. British Mycol. Soc.* **1985**, *85*, 223–238. [CrossRef]
43. Liro, J.I. Uredinae Fennicae: Finnlands rostsvampar. *Bidr. känned. Finl. natur folk.* **1908**, *65*, 642. (In Swedish).
44. Petäistö, R.-L.; Kurkela, T. Life cycle of *Melampsora larici-epitea* on short rotation cultures of *Salix burjatica*. *Scand. J. For. Res.* **1996**, *11*, 406–409. [CrossRef]
45. Kurkela, T.; Jalkanen, R. Checklist of the rust species recorded on trees in Finland. In Metsäntutkimuslaitoksen tiedonantoja, Proceedings of the First IUFRO Rusts of Forest Trees Working Party Conference, Saariselkä, Finland, 2–7 August 1998; Jalkanen, R., Crane, P.E., Eds.; The Finnish Forest Research Institute: Rovaniemi, Finland, 1998; Volume 712, pp. 15–18.
46. Poteri, M. *Screening of Birch, Betula spp., for Rust Resistance to Melampsoridium Betulinum*; Research Papers; Finnish Forest Research Institute: Helsinki, Finland, 1998; Volume 689, p. 44.
47. Kurkela, T.; Hanso, M.; Hantula, J. Differentiating characteristics between *Melampsoridium* rusts infecting birch and alder leaves. *Mycologia* **1999**, *91*, 987–992. [CrossRef]
48. Klebahn, H. *Die Wirtswechselnden Rostpilze*; Borntraeger: Berlin, Germany, 1904; p. 447. (In German)
49. Jalkanen, R. Lepänruoste pyyhälsi halki Suomen. *Metsälehti* **2003**, *8*, 55. (In Finnish)
50. Kurkela, T.; Hanso, M.; Hantula, J. *Melampsoridium* sp. on alder leaves. In Metsäntutk.imuslaitoksen Tiedonantoja, Proceedings of the First IUFRO Rusts of Forest Trees Working Party Conference, Saariselkä, Finland, 2–7 August 1998; Jalkanen, R., Crane, P.E., Eds.; The Finnish Forest Research Institute: Rovaniemi, Finland, 1998; Volume 712, pp. 131–134.