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What happens with the tree rings when the bird-cherry (*Prunus padus* L.) is defoliated by the moth bird-cherry ermine (*Yponomeuta evonymellus* Linnæus, 1758)?

Helena Åström & Carl-Adam Hæggström

Åström, H., Organismal and Evolutionary Biology Research Programme, Faculty of Biological and Environmental Sciences, P.O. Box 65, FI-00014 University of Helsinki, Finland. E-mail: helena.astrom@helsinki.fi
Hæggström, C.-A., Finnish Museum of Natural History, Botany Unit, P.O. Box 7, FI-00014 University of Helsinki, Finland. E-mail: aba.haeggstrom@gmail.com

The anatomy of a *Prunus padus* tree which was totally defoliated by the moth bird-cherry ermine *Yponomeuta evonymellus* in 2013, was compared with a tree without the moth infestation. After been defoliated by *Y. evonymellus* larvae, the infested *P. padus* developed new leaves from the next year's winter buds. These leaves grew so close to one another that they formed almost a leaf rosette. Consequently, the internodia of the branches were very short forming vegetative dwarf branches. In the normally developed tree, the leaves were located about 2 cm from one another on the branches.

The secondary xylem of *Prunus padus* is diffuse-porous or weakly ring-porous with the large vessels spread almost evenly throughout the tree ring or located together in irregular groups. The majority of the cells are lignified fibres. As a result of the infestation, the tree ring became narrower and the fibres in the middle part of the tree ring were not lignified properly. In the wood formed late during the season or in the tree ring formed during the following year the cell walls were lignified and thicker. Although this study includes only one studied infested *P. padus* tree, the effects of the infestation and defoliation is clear, and can be traced both in the morphology and the wood structure of the stem

Introduction

The bird-cherry *Prunus padus* L. is one of the common domestic tree species in Finland. It is distributed throughout the country with the least frequent occurrence in Lapland (Lampinen & Lahti 2018). Two subspecies have been distinguished in Finland: *P. padus* subsp. *padus* occurring in most of the country and *P. padus* subsp. *borealis* (Wimm. & Graebn.) Nyman occurring in northern Finland (Raatikainen 1991, Hämet-Ahti et al. 1992, 1998). Intermediate specimens between the subspecies seem to be common (Kujala 1965).

Prunus padus is often infested by the host specific moth bird-cherry ermine (*Yponomeuta evonymellus* Linnæus, 1758) (Leather 1985, Väisänen & Heliövaara 1991, Hyönteiskartoitus / Insektkartering 81 1992–1996b). The young larvae hibernate inside the egg on the host tree

(Kankaanhuhta et al. 2003). Young larvae begin their life as leaf miners, but later they live gregariously on the leaves and branches of the host tree inside a silk web. A heavily infested tree will be totally covered by this web. The first traces of silk web can be seen in southern Finland in the latter part of May. If the infestation is heavy, the *P. padus* trees will be defoliated. The larvae pupate in bunches in the web in July and the adult moths appear a few weeks later. Occasionally, the same tree may be infested during two following years (Raatikainen 1991). It seems, however, that the infested tree survives the two defoliations.

The heavy infestations take place with some years' intervals. The infestations of *Y. evonymellus* were monitored from 1981 onwards (Väisänen & Heliövaara 1991, Hyönteiskartoitus / Insektkartering 81 1992–1996b, Alonso et al. 2000). The infestations were heavy and frequent, especially in western Finland in 1981 (Leather & Lehti 1982). The infestations became, however, rarer during the following years, being quite scarce in 1984 to 1989 (Väisänen & Heliövaara 1991). During the early 1990s, the infestations were moderate or even strong, chiefly in the southernmost part of Finland (Hyönteiskartoitus / Insektkartering 81 1992–1994), but they declined to almost nothing in 1995 and 1996 (Hyönteiskartoitus / Insektkartering 81 1996a, 1996b).

The heavy infestations do not occur simultaneously in the whole country, although *P. padus* may be affected in large areas in some years. During later years, heavy infestations were seen in South Ostrobothnia in 2011 (Yle 2011), in Kainuu in 2014 and 2016 (Manninen 2014, Kaleva 2016), and in eastern Helsinki in 2016 (Metro 2016).

The infestation in southern Finland was irregular in 2013, with many trees totally defoliated, whereas other trees next to those infested were hardly affected at all or even without a single larva of *Y. evonymellus*. As *P. padus* leaves contain various amounts of protective compounds, all trees in an area are not infested by *Y. evonymellus* (Uusitalo 2004).

When a *P. padus* tree is totally defoliated in June, its growth will stop. After some weeks, the apical and lateral buds are beginning to develop into new shoots with fresh leaves. Thus, the tree will have a fully developed foliage in August.

When the growth stops, there will be no further development of that year's annual tree ring for several weeks. What happens with the tree ring? Will there be a new ring when the growth continues or will the growth of the ring continue? To answer this question, we did a case study of the tree rings of a *P. padus* tree which was totally defoliated in June 2013.

Material and methods

Four *Prunus padus* trees in the Åland Islands and two in Esbo were sampled for suitable material for our study. As the trees in Åland were only partly defoliated by *Yponomeuta evonymellus* they were not well suited for the study. Thus, two trees only in Esbo were used.

Tree 1. An about 8–9-m-high tree at the W side of the small hill Gruvberget in Kilo (coordinates with 10 m accuracy, according to the Uniform Coordinate System (UCS) Grid 27 °E, 668149: 337801). The tree was totally defoliated in June 2013. The tree had new leaves in late August, 2013. Samples of twigs were taken on August 30, 2013 and November 11, 2013. The tree was not infested by *Y. evonymellus* in 2014 and we took new samples of twigs on October 28, 2014.

Tree 2. An about 8-9-m-high tree in Karabacka in Kilo (UCS 668171:337664). The tree was unaffected by *Y. evonymellus* in 2013. Samples of twigs were taken on September 2 and November 11, 2013.

The twigs were fixed and preserved in FAA (formalin-acetic acid-alcohol) solution (36% paraformaldehyde (ProLabo), 100% acetic acid (Merck), 50% ethanol; 5:5:90 by volume). The twigs were embedded in Jung Tissue Freezing Medium prior to the cryosectioning. Serial sections of the twigs 14-30 µm thick were cut with an ice cryotome (Leica CM3050/S; GmbH, Germany). The sections were stained with an 0.5 % aqueous solution of alcian blue (National Diagnostics, USA), followed by 0,5% safranin O (Merck KGaA, Germany) in 50 % ethanol. The microscope slides were mounted with Canada balsam (Merck), dried and then examined and photographed using a Leica DMLB light microscope with an attached camera (Leica DFC 490).

Results

The leaves of *Prunus padus* are spirally arranged (leaf position 2/5). In a normally developed tree, the leaves are located about 2 cm from one another on the branches (Leather 1996) (Fig. 1). In a defoliated tree, the young terminal and axillary winter buds, which should develop next year, will develop already a few weeks after the defoliation. The internodes of these new branches are very short and the leaves are located so close to one another that they form almost a leaf rosette (Fig. 2). Thus, *P. padus* develops vegetative dwarf branches after defoliation. (The racemes with flowers are generative dwarf branches). The effect of the defoliation on the habitus of the infested *P. padus* stem is shown in Fig. 3. The leaf scars are located close to each other in the stem section of the year 2013 and thus the total length growth of the stem is only about 1 cm. The length of the stem sections during the previous and following year have normal long internodes and the yearly length increment is 14 cm in 2012 and 6,5 cm in 2014 in the branch studied.

Fig. 1. A normally developed branch of *Prunus padus* (tree 2). The leaves are alternate with a distance of about 2 cm from one another. In late summer, the leaves are worn with holes and other traces of herbivory. – Esbo, Kilo, Karabacka, September 2, 2013. Photo: C.-A. Hæggström

Fig. 2. A branch of *Prunus padus* (tree 1) which was totally defoliated by *Yponomeuta evonymellus* larvae in June, 2013. Traces of the silk of the larvae are visible on the branch. The winter buds of 2014 developed a few mm long dwarf branches with fresh and undamaged leaves forming almost a rosette. The leaf scars of the eaten leaves can be seen below the new leaves. New winter buds are located in the terminal ends of each dwarf branch. – Esbo, Kilo, Gruvberget, August 29, 2013. Photo: C.-A. Hæggström.

Fig. 3. A branch, representing the years 2012–2014, of the defoliated *Prunus padus* tree no. 1, collected in December 2015. The dwarf shoot of 2013 is approx. 1 cm long with two sets of aggregated leaf scars. The shoot of 2012 is about 14 cm long with 1.5 to 3 cm long internodes, whereas the shoot of 2014 is 6.5 cm long with 1 to 1.5 cm long internodes. Photo: C.-A. Hæggström.

Table 1. The thickness of the bark, the width of the tree rings and pith of two five-year-old branches of *Prunus padus* tree no. 1. The measurements, given in mm, were measured along two perpendicular diameters A–B and C–D, where A represents the adaxial and B the abaxial side.

	Branch 1		Branch 2	
	Diameter A–B	C–D	Diameter A–B	C–D
Pith	1.57–1.65	1.36–1.62	1.50–1.60	1.50–1.60
Tree ring 2010	0.65, 0.59	0.57, 0.71	0.62, 0.60	0.57, 0.70
Tree ring 2011	1.69, 0.95	1.38, 1.25	1.61, 0.95	1.23, 1.56
Tree ring 2012	0.68, 0.53	0.58, 0.64	0.66, 0.56	0.58, 0.72
Tree ring 2013	0.45, 0.39	0.34, 0.40	0.42, 0.42	0.34, 0.41
Tree ring 2014	0.53, 0.52	0.50, 0.52	0.53, 0.54	0.48, 0.48
Bark	0.72, 0.77	0.72, 0.76	0.79, 0.80	0.74, 0.84

According to Leather (1996), the shoot growth and the bud set are usually completed in Great Britain by the end of July. This was not the case in Finland in tree 1 in 2013, as its growth was not completed in late August, partly due to the warm weather with good precipitation continuing well to the end of September (Ilmastokatsaus 2013).

As the twigs of tree 1 grew more or less horizontally they have developed tension wood with the adaxial side of the twigs more strongly developed than the abaxial side (Table 1).

The tree rings show the following features (Table 1):

2010 – the ring is between 0.57 and 0.71 mm wide which seems to be a normal width.

2011 – the ring is wider than any of the other studied with a width of 0.95 to 1.69 mm. This may be a result of the warm weather with good precipitation during the growth period (Ilmastokatsaus 2011).

2012 – the ring seems to be of normal width, 0.53 to 0.72 mm.

2013 – the growth of the tree ring ceased when the tree became defoliated. Later the development of the tree ring continued, but the growth was weak and the lignification was very weak. This ring is the narrowest with a width of 0.34 to 0.45 mm

2014 – the ring is quite narrow, 0.50 to 0.54 mm, perhaps due to the stress of the previous year's defoliation.

The secondary xylem of *P. padus* is diffuse-porous or weakly ring-porous (Scholz & Scholz 1995, Fagerstedt et al. 2016) with the large vessels spread almost evenly throughout the tree ring or located together in irregular groups. The majority of the cells are lignified fibres (Fig. 4). As a result of the infestation in 2013, the tree ring seen in the section from a five-year-old branch of

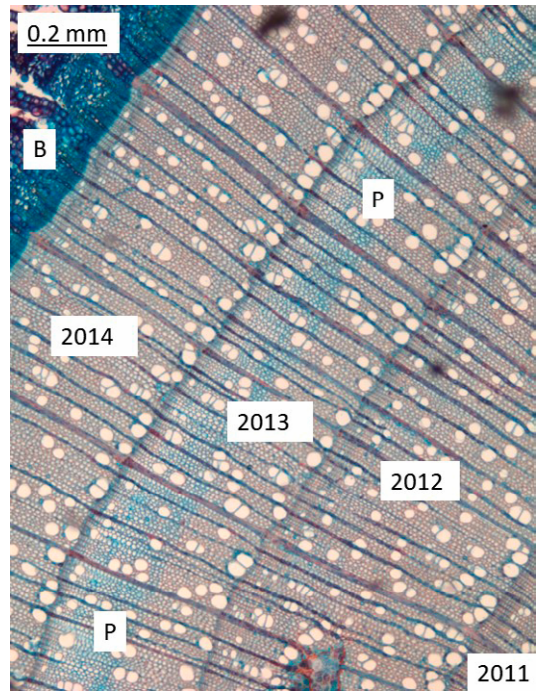

Fig. 4. A section of a five-year-old branch of *Prunus padus* tree no. 1. The four tree rings represent the years of 2011, 2012, 2013 and 2014, followed by the bark (B). The tree was defoliated in June 2013 and the tree ring is narrower than the adjacent ones. The late wood fibres are chiefly parenchymatous (P, blue colour instead of the reddish coloured lignified wood fibres). The radial stripes are pith rays. Microphoto: Helena Åström.

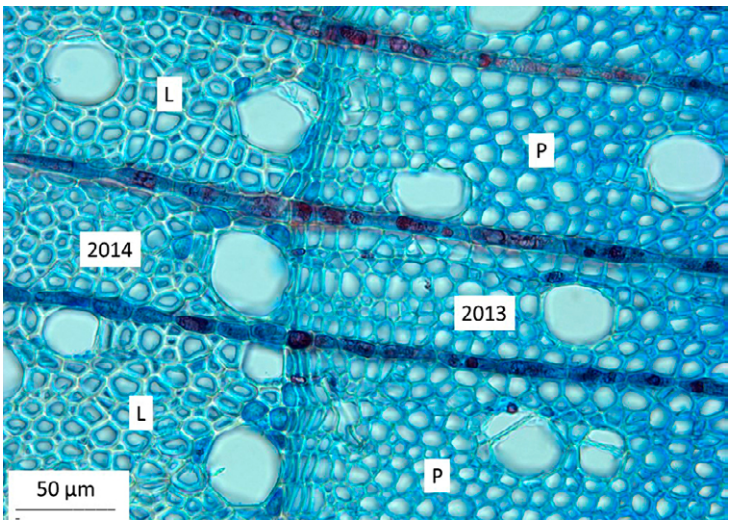

Fig. 5. Detail of the border between the tree ring formed during the summer 2013 and the tree ring of 2014. The fibres in the middle of the tree ring of 2013 are thin-walled and coloured blue (marked with P). In the tree ring of the following year the cell walls of the fibres are lignified and thicker (marked with L). Due to the magnification, the reddish colour indicating lignified fibres cannot be discerned. Three pith rays are seen as blue rows of cells. Microphoto: Helena Åström.

P. padus is narrower and the fibres in the middle part of the tree ring are not lignified properly. There is a clear difference between the staining of the fibres in the wood formed during infestation, compared with the fibres in the early wood, and in the wood formed later during the growing season (Fig. 4). This can be seen as a result from the used staining procedure; the fibres in the wood formed during the infestation are thin-walled and the cell walls are stained blue (Fig. 5). In the wood formed late during the season or in the tree ring formed during the following year the cell walls are lignified and thicker. No clear difference between the larger vessels or their cell wall thickness formed during the infestation and afterwards can be seen.

Experimental defoliation of *P. padus* has shown that the growth of the trees is hampered compared to unaffected ones (Leather 1995). The defoliation can be seen in the development of the tree rings. The tree ring of the infestation and defoliation year has a thinner tree ring with incomplete lignification of the cell walls of the tree fibres. The infestation and defoliation can thus be traced in the morphology and the wood structure of *P. padus* stems. Several infestations are probably weakening the wood of *P. padus* due to incomplete or lacking lignification of the tree rings.

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Discussion

After been defoliated by *Yponomeuta evonymellus* larvae, infested *Prunus padus* develops new leaves from the next year's winter buds. These leaves grow so close to one another that they form almost a leaf rosette. Consequently, the internodia of the branches are very short forming vegetative dwarf branches.

The infestation can clearly be seen later on in the structure of the branches as the leaf scars are located very closely to one another. Thus, it is possible to see former defoliations due to *Y. evonymellus* by studying the leaf scars on branches of *P. padus*.

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