

Oviposition preference and larval performance in gall-inducing sawflies

Trond Elling Barstad¹, Arne C. Nilssen¹ and Sanna Leppänen²

¹Department of Natural Sciences, Tromsø University Museum, NO-9037 Tromsø, Norway

² Pikisaarekatu 40 as 10, 53900 Lappeenranta, Finland

Corresponding author:

Trond Elling Barstad

Department of Natural Sciences, Tromsø University Museum, NO-9037 Tromsø, Norway

E-mail: trond.elling.barstad@uit.no

Telephone: +47 776 45 027

Abstract

The relationship between female ovipositional preferences for high quality food resources that enhance larval performance, has received considerable attention in the study of plant and herbivore interactions. It predicts that female choice should be beneficial for larval performance. However, not all studies support this preference-performance linkage, especially among leaf-galling sawflies. Oviposition preference was examined in relation to larval performance in three congeneric gall-inducing sawfly species (Tenthredinidae: Nematinae: *Pontania nivalis*, *P. glabrifrons* and the previously studied *P. arcticornis* acting as a reference species) from northern Norway. All are commonly found on their willow host (*Salix* spp.). Mortality caused by parasitoids was also investigated. Random samples of shoots with galls were collected in late August from Komagdalen and Ifjordfjellet (2008 and 2009) and Nakkedalen (2012 and 2013). Shoot length and node position oviposition preferences (all sites and years), larval performance (i.e. late stage larval mortality) and mortality caused by parasitoids (only for Komagdalen and Ifjordfjellet, 2008 and 2009) was recorded. Oviposition preference for short shoots and low node position was shown for all three *Pontania* spp.. We found no preference that would enhance performance, as there were no differences in oviposition preference and larval performance when comparing living and dead late stage larvae. This seems to be caused by early spring oviposition when there is an absence of cues for females having any discriminatory behaviour. In addition, the survival rates of the three *Pontania* spp. were high and mortality caused by parasitoids was low (mean = 8.7 %, other mortality, mean = 16.7 %), corroborating results in other Arctic studies.

Keywords: Oviposition preference, larval performance, *Pontania*, plant vigor hypothesis, plant constraint hypothesis, *Salix*, parasitoids.

Introduction

The abundance and population dynamics of herbivorous insects living in the harsh and unpredictable Arctic environment are in general poorly known. Many adaptation requirements are needed in order to survive, and northern populations are considered to fluctuate more than those found further south, due to the environmental severity (Danks 1981, 1986, 1987, 2004; Humble 2006; Ring and Tesar 1981; Strathdee and Bale 1998). Biological factors are assumed to be less important than physiological factors (Danks 1981, 1986), and spatial and temporal variation in suitable host plant resources can severely affect the insects' performance during the short Arctic summer (Clancy and Price 1986; Danks 1981; Downes 1965). An important phenological event among many herbivorous insects in the Arctic is the evolutionary fine-tuned synchronous spring eclosion, which often occurs in synchrony with host plant leaf flush suitable for oviposition and larval development (Danks 1986, 2004; Singer and Parmesan 2010; Tauber et al. 1986; Volney and Fleming 2000). Outside this window of opportunity, the host plant sets constraints on larval performance and survival as the plant resource quality deteriorates (Hanhimaki et al. 1995; Hunter 2000; Hunter and Elkinton 2000; Martel and Kause 2002; Mopper 2005). Therefore, oviposition preference of herbivorous insects has evolved to optimize larval performance, in which higher plant resource quality is chosen. The relationship between oviposition preference and larval performance are important aspects in understanding plant-insect interactions and population dynamics of herbivorous insects (Price 2003).

Most studies involving herbivorous insects in relation to plant vigor (i.e. plant module growth rate), oviposition preferences and larval performance, have been carried out with gall-inducing insects (Cornelissen et al. 2008; Price 2003; Price et al. 2004). Shortly after eggs are laid, gall formation is provoked (Kopelke 1985b, 1999; Viitasaari 2002). Female preference for certain plant module size or growth rate can influence gall induction success, as well as fitness and survival of the larvae inside the gall (Craig et al. 1989; Price 1991, 2003; Price et al. 2004; Price et al. 1987b; Quiring et al. 2006).

Herbivorous insects that live in the Arctic are mostly oligophagous or polyphagous (Danks 1981; Downes 1965; Strathdee and Bale 1998). However, gall-inducing

sawflies (Tenthredinidae: Nematinae) commonly found on their willow host (*Salix* spp.) are strictly monophagous, with only a few exceptions (Kopelke 1991; Kopelke 1994; Kopelke 1999; Viitasaari 2002; Vikberg 1970). They are widely distributed throughout the Holarctic region, and willows, the main host plants, are distributed well into the Arctic (Zinovjev 1998). Gall-inducing sawflies are highly adapted to the Arctic environment and found at high densities as far north as 72 °N in the Palearctic (Roininen et al. 2002; Roininen et al. 2005). This may be due to the general pattern among gall-inducing sawflies to prefer oviposition on vigorous growing, long shoots, a habit that increases larval performance (Craig et al. 1989; Hjältén et al. 2003; Price 1991, 2003; Roininen and Danell 1997). This preference-performance linkage is possibly the strongest described in herbivorous insects (Craig et al. 1989; Price et al. 2004), and is probably critical among Arctic populations due to the short summer in which larval development must occur (Danks 1986).

The general oviposition preference and the larval performance pattern shown among gall-inducing sawflies have generated the plant vigor hypothesis, which suggests that there is a fitness advantage for larvae living on vigorous plant modules which derive from female oviposition choice (Price 1991). The hypothesis predicts that there is an oviposition preference for a large or fast growing plant module in which a preference-performance correlation would be detected based on plant module choice (i.e. higher fitness and survival) (Price 1991, 2003). In addition, the plant constraint hypothesis suggests that the female saw-like ovipositor is constrained to oviposit into specific soft host plant resource, matching host plant phenology of young plant growth (Price 1994; Price et al. 2004).

The preference-performance pattern can be tested using a simple, general approach by comparing plant heterogeneity (i.e. a chosen plant module size) with the response of herbivores (i.e. preference and performance). Thus, the herbivore attack in relation to plant module size reflects female oviposition preference, and the response in larval performance and survival pattern can be detected prior to diapause in autumn (Price 1991). Using patterns in shoot length variation and node position (leaf position on the shoot on which the female oviposits and in which gall formation occurs) of herbivore attack is an important host character to which herbivores respond (Craig et al. 1989).

The summary in Price (2003) shows that the preference-performance linkage is common among sawflies within stem- and bud-galling *Euura*, leaf rollers *Phyllocolpa*, stem borers *Ardis*, free-feeding *Nematus* and some other genera (Cornelissen et al. 2008; Price 2003). However, non-conformist species with regard to the plant vigor hypothesis have been detected, mostly among the leaf galls *Pontania*, which show no ovipositional preferences for long, vigorous growing shoots or in relation to higher larval and adult survival. Among 44 gall-inducing sawfly species that have been studied with regard to the plant vigor hypothesis, seven species do not fit this pattern, including *Pontania arcticornis* studied in the present paper (Price 2003; Price et al. 2004), all of which show no ovipositional preferences that enhance larval performance.

When larval development is complete in late August (Barstad and Nilssen 2015), the larvae start preparing for overwintering hibernation (i.e. diapause). This occurs in response to a *token stimulus*, photoperiod, in which *Pontania* spp. synchronously emerge from the gall in September (Barstad and Nilssen 2016). In general, all *Pontania* spp. larvae emerge from galls after finishing larval development and pupate on the ground (Kopelke 1999; Wagner 1993; Zinovjev 1998). Barstad and Nilssen (2016), however, detected that some the larvae do not emerge from the galls to pupate, and instead pupate inside the gall. This phenomenon has not previously been studied, and although there is no clear explanation for this behaviour, it may be due to poor host quality. Shoots that have low growth rate may be of poor quality, thus prolonging larval development that shortens the window of opportunity for emerging from galls in search for overwintering sites on the ground.

Factors other than plant-attributed mortality due to poor performance that may have great impact on population dynamics, are natural enemies such as parasitoids. Natural enemies can suppress population survival and disrupt population dynamics, and may be an important mortality factor among insects in the Arctic (Danks 1986, 2004). However, contrasting results from Arctic insects have been shown (Clancy and Price 1986; Kukal and Kevan 1987; Roininen and Danell 1997; Roininen et al. 2002). Parasitoids, which kill their host, are common among gall-inducing sawflies (Kopelke 1985a; Kopelke 1985b; Kopelke 1994; Kopelke 1999; Roininen and Danell 1997; Roininen et al. 2002). Mortality caused by parasitoid species assemblage and attack

frequency have, however, been shown to decline at higher latitudes and may have less impact on survival on gall-inducing sawflies (Kopelke 1985a, 1994; Price and Pschorn-Walcher 1988; Roininen et al. 2002).

This study investigated the oviposition preference and larval performance pattern for three common congeneric monophagous gall-inducing *Pontania* spp. on their willow host in northern Norway. These *Pontania* spp. are highly adapted to the harsh environmental conditions in the Arctic (Barstad and Nilssen 2012; Hjältén et al. 2003; Humble 2006; Miller and Werner 1980; Ring and Tesar 1981; Roininen et al. 2002; Zinovjev 1998). We hypothesized that, 1) the not previously studied gall-inducing sawfly species, *Pontania nivalis* and *P. glabrifrons* were non-conforming species in relation to the plant vigor hypothesis (sensu Price et al. (2004)), with no oviposition preference for vigorous plant modules, or larval performance benefits (i.e. having similar larval performance pattern across plant modules chosen). 2) We also investigated the phenomenon of pupation inside the gall in relation to the common pupation outside the gall, in relation to the above mentioned oviposition preference pattern and hypothesized that this may be due to poor host quality (i.e. short shoots), and 3) That parasitoids have low impact on mortality, and that the overall mortality is low in accordance with other Palearctic studies.

Material and methods

The focal species and field sites

Leaf-galling sawflies (Tenthredinidae: Nematinae) are highly adapted to the Arctic environment, and commonly found on their willow host in northern Norway (Barstad and Nilssen 2012; Hjältén et al. 2003; Roininen et al. 2002; Zinovjev 1998; Zinovjev and Vikberg 1999). Three monophagous congeneric *Pontania* species within the viminalis-group were included in this study, *Pontania nivalis* (Vikberg 1970), *P. glabrifrons* (Benson 1960), *P. arcticornis* (Konow 1904) and were found on *Salix glauca*, *S. lanata* and *S. phylicifolia*, respectively. They have an obligate univoltine life cycle and induce a pea-shaped gall on underside of the leaf, which occurs in early spring after a short period of mating and ovipositing on young leaves. While ovipositing, the female injects an unknown secretion that stimulates gall-formation.

Further on gall growth is enhanced by a secretion during larval feeding. Larval feeding ceases when larval development has ended (Zinovjev 1993; Zinovjev 1998). The larvae emerge from galls in the autumn to pupate as prepupae on the ground among leaf litter (Knerer 1993; Kopelke 1999; Price 2003; Viitasaari 2002; Wagner 1993; Zinovjev 1993; Zinovjev 1998).

The field sampling was conducted over four years at three study sites in northern Norway (Fig. 1). , Two sites were at 70 °N, in Finnmark County, Komagdalen (70 °N, 30 °E), one on the Varanger Peninsula and one 100 km to the west, Ifjordfjellet (70 °N, 27 °E) in 2008 and 2009. Both sites exhibit Arctic climatic condition (<10 °C Arctic isotherm) and are classified as erected shrub tundra (Henden et al. 2011; Virtanen et al. 1999; Walker et al. 2005). The third study site, Nakkedalen (69 °N, 19 °E), Troms County was studied in 2012 and 2013, and exhibits a sub-Arctic climate with mixed vegetation of willow shrubs (*Salix* spp.) and birch trees (*Betula* spp.).

Data acquisition and analyses

Shoot length and node position preferences in relation to larval performance

To determine oviposition preference and larval performance, random samples of shoots with *Pontania-viminalis* galls from different clones were collected in late August from *S. glauca*, *S. lanata* and *S. phylicifolia* [Total $n = 2343$, *S. glauca* ($n = 574$), *S. lanata* ($n = 831$) and *S. phylicifolia* ($n = 938$)] at Komagdalen, Ifjordfjellet and Nakkedalen (details in supplementary Tab. 1). Oviposition preference data were then recorded, including shoot length (mm) (shoots with 1 gall), node position (leaf with gall counting from proximal towards distal end of shoot), and number of nodes (total number of leaves). To assess performance (i.e. survival), shoots with galls were placed in single plastic cups with peat moss (*Sphagnum* spp.) (155 ml, with ventilation holes) and stored under natural outdoor conditions. In September, larval emergence from galls was monitored once a day. Performance (i.e. survival) was classified as 1) living late stage larvae (presence of emergence holes in a gall or observed larvae outside gall) and 2) dead late stage larvae (absence of emergence hole in gall). According to Craig et al. (1989), this accurately reflects performance (i.e. survival). However, not all larvae leave the gall to pupate, but rather pupate inside the

gall. In order to assess the occurrence of this adaptation, galls were dissected after initiation of pupation and winter dormancy. This also detected any occurrence of parasitoid attack (see section below). Comparisons of oviposition preference (i.e. shoot length and node position) between late stage larvae that emerge from gall and those that do not, were made using the Generalized linear models (GENLIN) in SPSS version 21. (Distribution: normal; Link: identity; Factor: species; Covariable: shoot length; Dependent variable: number of leaves.)

Parasitoid attack and mortality

The absence of emergence holes on galls was classified as mortality, indicative of dead late stage larvae. This was recorded during the pre-diapause period in September. These galls were dissected after the period of pupation and overwintering hibernation had occurred, to assess the rate of parasitoid attack (parasitoid pupae detected either inside gall or inside *Pontania* spp. pupae inside the gall). Mortality factors, classified as unknown cause of death and death caused by parasitoid attack, were investigated at Ifjordfjellet and Komagdalen (2008, 2009) [Total $n = 1985$, *P. nivalis* ($n = 497$), *P. glabrifrons* ($n = 800$) and *P. arcticornis* ($n = 688$)]. An additional, more time efficient method was used to detect parasitoid attack for Komagdalen in 2009 (Fig. 5a and supplementary Tab. 2). Late-stage galls were dissected and sawfly larvae were inspected under microscope in order to detect parasitoid larvae and to assess mortality factors (death caused by parasitoid attack and unknown cause of death) [Total $n = 2796$, *P. nivalis* ($n = 338$), *P. glabrifrons* ($n = 952$) and *P. arcticornis* ($n = 1506$)] (details in supplementary Tab. 2).

Results

Shoot length and node position preferences in relation with larval performance

The mean *Pontania* spp. larval survival rate (classified as number of galls with emergence holes) was 71.9 % (total $n = 1684$) [*P. nivalis* 67.6 % ($n = 388$), *P. glabrifrons* 73.8 % ($n = 692$), *P. arcticornis* 72.7 % ($n = 604$)] and ranged from 30.2 % to 89.7 % (details in supplementary Tab. 1).

Shoot length preferences showed similar pattern for the three *Pontania* spp., with the highest preference for shorter shoots (Fig. 2). There were, however, significant differences between the species (supplementary Fig. 1). Shoot length ranged between 5-200 mm, mean = 53.7 mm (*P. nivalis* on *S. glauca*), 10-200 mm, mean = 68.4 mm (*P. glabrifrons* on *S. lanata*) and 5-315 mm, mean = 78.1 mm (*P. arcticornis* on *S. phylicifolia*). A similar pattern was evident for node position preferences for the three *Pontania* spp., with highest preferences for lower node position (Fig. 3), but there were significant differences between the species (supplementary Fig. 1). Node position ranged between 1-12, mean = 4.58 (*P. nivalis* on *S. glauca*), between 1-15, mean = 5.62 (*P. glabrifrons* on *S. lanata*) and between 1-18, mean = 3.39 (*P. arcticornis* on *S. phylicifolia*). Comparison between shoot lengths and node position preferences showed high correlation, i.e. longer shoots had higher node positions for all three species (Fig. 4). There were, however, no significant differences in preference patterns in both living (emergence holes in gall) and dead late stage larvae (no emergence hole in gall) (i.e. survival) in relation to shoot length and node position preferences among the three *Pontania* spp. (Fig. 2 and 3) (also see supplementary Fig. 2a, b and c).

There were no significant differences in shoot length or node position preferences in the occurrence of pupation inside the gall at Komagdalen and Ifjordfjellet in 2008 and 2009, compared to pupation outside for each *Pontania* spp. (supplementary Figs. 2a, b and c, and supplementary Fig. 3). Occurrence of pupation inside gall was for *P. nivalis* 17.8 % (min 15.1 %, max 20.8 %), for *P. glabrifrons* 17.0 % (min 14.1 %, max 21.0 %), and for *P. arcticornis* 8.9 % (min 5.6 %, max 15.1 %) (details in supplementary Tab. 2).

Comparison between shoot length and number of nodes (i.e. total number of leaves on shoots), showed high correlation for all *Salix* spp. ($p < 0.0001$), however significantly different between the species (supplementary Fig. 4, supplementary Fig. 1). Number of nodes (i.e. number of leaves) on shoots ranged between 2-14, mean=6.9 (*S. glauca*), between 2-20, mean=8.9 (*S. lanata*) and between 2-21, mean=7.6 (*S. phylicifolia*).

Mortality caused by parasitoids

Mortality factors, parasitoids (not identified, but species from Ichneumonidae, Braconidae and Pteromalidae) (Kopelke 1985a; Roininen et al. 2002), unknown mortality and total mortality was investigated at Komagdalen and Ifjordfjellet in 2008 and 2009. The mortality for the three *Pontania* species ranged from 7.7 % to 34.5 % (mean = 25.4 %) (*P. nivalis*, mean = 31.5 %, *P. glabrifrons*, mean = 22.5 % and *P. arcticornis*, mean = 19.3 %). Parasitoid attack ranged from 2.6 % to 16.1 % (mean = 8.7 %) (*P. nivalis*, mean = 12.3 %, *P. glabrifrons*, mean = 10.9 % and *P. arcticornis*, mean = 4.1 %). Unknown mortality ranged from 5.1 % to 21.4 % (mean = 16.7%) (*P. nivalis*, mean = 21.1 %, *P. glabrifrons*, mean = 11.0 % and *P. arcticornis*, mean = 15.2 %) (details in supplementary Tab. 2).

Comparisons of mortality rates caused by parasitoids and otherwise between species within the same site and year, were made using G-tests in the online resource (www.biostathandbook.com/gtestgof.html). There was a significant difference in mortality caused by parasitoids at Ifjordfjellet 2009 only, and *P. arcticornis* was significantly lower from *P. nivalis* and *P. glabrifrons* ($p = 0.018$ and $p = 0.005$, respectively). Other mortality, was only significantly different between *P. nivalis* and *P. arcticornis* ($p = 0.022$), Ifjordfjellet 2009. No significant difference was found for *Pontania* spp. in Komagdalen 2008 and 2009a and b (Fig. 5a).

In addition, comparisons of mortality rates between years and species at the same site (Ifjordfjellet 2008-2009 and Komagdalen 2008-2009) are inconclusive. Only mortality caused by parasitoids and other mortality (G-test), among *P. arcticornis*, Ifjordfjellet 2009, differed significantly from all other combinations. The mortality of all species from Ifjordfjellet 2008 was significantly different from all species in 2009, whereas at Komagdalen 2008 and 2009, the only significant difference was between *P. nivalis* 2009 and *P. glabrifrons* and *P. arcticornis* 2008. Other mortality causes were not significantly different for Komagdalen and both years (Fig. 5b)

Discussion

Host-plant quality determines fitness and survival during larval development among many insects, and the oviposition preference-larval performance linkage for gall-inducing sawflies is one of the strongest shown (Craig et al. 1989; Price et al. 2004). However, there are some leaf-galling species within the *Pontania-viminalis* group that do not follow this pattern. The present study showed that *P. nivalis*, *P. glabrifrons* and *P. arcticornis* have no preference for vigorous growing shoots or preferences enhancing larval performance (i.e. survival). Hence, we can add two not previously studied species to the list of non-conformist species (i.e. species that do not have any oviposition preference-larval performance linkage enhancing larvae survival) given by Price (2003) (see also Price et al. (2004)). However, *P. arcticornis* has previously been added to the list, mistakenly named *P. arctica* in Price (2003) (Price et al. 2004), and acts as a reference species in the present study.

The strong preference-performance linkage shown for gall-inducing sawflies has been comprehensively studied (Carr et al. 1998; Cornelissen et al. 2008; Craig et al. 1989; Craig et al. 1990; Hjältén et al. 2003; McGeoch and Price 2004; Price and Craig 1984; Price 1991, 1994, 2003; Price et al. 2004; Price et al. 1987a, b, 1997; Roininen et al. 1988; Santos et al. 2008) resulting in the plant vigor hypothesis (Price 1991). This hypothesis proposes that there is a natural selection on female oviposition choice, with oviposition on large, vigorously growing plant modules (i.e. shoots) resulting in increased larval fitness (i.e. survival) (Price 1991, 2003). In addition, the plant constraint hypothesis suggests that for sawflies with an ovipositor shaped like a saw, oviposition is limited to certain plant tissue and phenologically synchronized with soft tissue on young host plants in which vigorous growing shoots are the best to oviposit on. However, a preference for a low-density plant resource may set constraints on availability during time of oviposition (Craig et al. 1986; Price 1994, 2003; Price and Carr 2000; Price et al. 1994). Among the 44 gall-inducing sawfly species that have been studied in regard to the above mentioned hypotheses, nine did not follow this pattern, including *P. nivalis*, *P. glabrifrons* and *P. arcticornis* (Price 2003; Price et al. 2004).

Price et al. (2004) proposed several explanations for the non-conformist species not following the plant vigor hypothesis. The present study showed that all three species had high survival rates and the same short shoot length preferences between living and dead late stage larvae (supplementary Tab. 1 and Fig. 2). High survival that is independent of shoot length preferences provides no feedback that may enhance larval survival. In addition, if there is little or no fitness advantage (i.e. enhancing larval survival) for oviposition on longer shoots, this would generate into a non-discriminative oviposition pattern. This may be due to the timing of oviposition, when the shoots with leaves cannot be distinguished from one another with regard to growth (Price 2004).

The eclosion phenology of non-conformist species occurs during a short period of time in early spring (Barstad and Nilssen 2015), in which oviposition cues are low or lacking, as suggested above. Results from Price (2003) and Price et al. (2004) indicate that *P. arcticornis* (included in the present study) and *P. mandshurica* oviposit in early spring on nodes independent of shoot length. This was also confirmed for *P. aestiva* (Price et al. 2004), which generated into a narrow range of node preference pattern (i.e. leaf position), also shown in the present study (Fig. 3). The node preference pattern reflects nodes available at time of oviposition. However, the present study showed significant correlation between shoot lengths and node positions (i.e. longer shoots had higher node positions). Node position may be related to oviposition phenology, as late oviposition naturally gives higher node position and a later gall formation. This pattern may be due to the female being constrained to oviposit on the youngest growing leaves. This is a result of leaves low on shoots may deteriorate (i.e. quality changes due to growth) as the oviposition period progresses, hence, leaves are unsuitable for oviposition. Low heterogeneity in leaf size, especially during time of oviposition, would also result in non-discriminative node preference pattern (Price et al. 2004), however not investigated in the present study. The available leaves (i.e. nodes) in early spring are low on the shoots, and as the shoot grows, leaves higher on the shoot become available (T. E. Barstad, unpublished). Hence, a narrow range of nodes low on shoots is used during early oviposition, and a larger range and higher on shoots during later oviposition. The short and early eclosion period was confirmed by Barstad and Nilssen (2015) for *P. nivalis* and *P. glabrifrons*, in which the eclosion period was approx. 20 days (although the majority

eclosed within a considerably shorter period of time). In contrast, conformist species have been shown to have a longer eclosion period of 30 days or more (Price and Craig 1984; Price and Carr 1986; Roininen 1991).

Larval emergence from gall prior to leaf abscission in autumn may also be important for survival, as shown for the stem-galling sawfly *Euura lasiolepis* (Craig et al. 1989). This was not confirmed for the leaf-galling *Pontania* spp., however, as they have been shown to survive as prepupae inside galls after leaf abscission (T. E. Barstad, unpublished): This may depreciate the survival feedback made by female oviposition preferences shown for conformist species (Craig et al. 1989).

Pupation inside the gall does seem to be very common for the three *Pontania* species (*P. nivalis* 17.8 %, *P. glabrifrons* 17.0 % and *P. arcticornis* 8.9 %), a fact that has not previously been observed or studied. No significant differences in host use preferences were detected when comparing pupation outside the gall. The three species follow the same pattern in shoot length and node position preferences, confirming the random attack pattern known for non-conformist species. There is no clear explanation for this phenomenon. One could speculate that this behaviour is due to lower larval fitness that might be caused by poorer food quality or other unknown factors, prolonging the larval development beyond the time window of opportunity for finding a place to pupate outside the gall. Prior to pupation, there is a sensitivity period during pre-diapause (i.e. late August) in which only mature larvae can respond to *token stimuli* (i.e. mainly photoperiod and secondary, temperature) (Barstad and Nilssen 2016). If larval development is prolonged, a mismatch occurs in the timing in which the larvae can respond to these *token stimuli*. This results in the subsequent pupation occurring later, and the larval response is to pupate inside the gall due to shortage of time to find suitable place on the ground to pupate. However, we lack information about their larval performance and survival in relation to larvae that pupate on the ground.

Little is known about the impact of predators and parasites on sawfly abundance, although there are a few studies of the degree of parasitism and parasitoid attack on larvae of gall-inducing sawflies in the Palearctic (Kopelke 1994; Kopelke 1999; Nyman et al. 2015; Roininen et al. 2002). Although the present study provided no

information about parasitoid assemblages or species attacking the three *Pontania* species, the mortality caused by parasitoids was similar to that found in other Palearctic studies. The Siberian study by Roininen et al. (2002) showed that *P. nivalis*, *P. glabrifrons* and *P. arcticornis* had high survival rates, 63.3, 56.2 and 80.4 %, respectively. Mortality rates caused by parasitoids were 17.9, 22.3 and 7.8 %, and other mortality causes were 18.9, 21.4 and 11.7 %, respectively, which are all in the same range as in the present study. Kopelke (2003) documented a similar parasitoid attack pattern (mortality caused by parasitoids = 23.1 % and other mortality causes = 19.1 %) for gall-inducing sawflies from the Arctic region of Fennoscandia, and for *P. nivalis*, *P. glabrifrons* and *P. arcticornis*, they were 21.0, 14.3 and 9.7 %, respectively. Both studies argued that the parasitoid assemblage was lower than in southern boreal regions resulting in the overall higher survival in the Arctic regions. The present study showed that the three *Pontania* species had high survival rates in which mortality caused by parasitoids was low (mean = 8.7 %, other mortality, mean = 15.0 %), corroborating the above-mentioned studies. The differences in survival rates between species, sites and years were also low, with *P. arcticornis* having the lowest rate of parasitoid attack. Another study (Nyman et al. 2015) in Tromsø, Norway, Abisko, Sweden and Kilpisjärvi, Finland showed similar results among seven *Pontania* species, but concluded that parasitoids were the main cause of death. Although the results for *P. nivalis*, *P. glabrifrons* and *P. arcticornis* only, deviates from the overall conclusion, in which death caused by parasitoids (mean = 16.9 %) was quite similar to other unknown causes of death (mean = 15.0 %) for the three *Pontania* spp. (Nyman et al. 2015). However, Nyman's study showed similar rates of parasitoid attack as in the present study and the above mentioned studies for *P. nivalis*, *P. glabrifrons* and *P. arcticornis*.

The present study adds two species, *P. nivalis* and *P. glabrifrons* to the list of non-conformist species presented by Price et al. (2004), and confirmed by *P. arcticornis* acting as a reference species (Price 2003). The three *Pontania* spp. had an oviposition preference for short shoots and low node position. We found no oviposition preference that enhanced larval performance (i.e. survival), as there were no differences when comparing living and dead late stage larvae. This is suggested to be caused by low heterogeneity (i.e. shoots and leaves) in the willow host resource during time of oviposition, when there is absence of cues that can result in any discriminating

behaviour enhancing larval performance. In addition, the short range of nodes oviposited on reflects the short oviposition period. The phenomenon of pupation inside galls has shown to be quite common, however showing no other host preferences for this behaviour. In addition, the three *Pontania* spp. had high survival rates in which mortality caused by parasitoids was low, corroborating other Palearctic studies. Together with our previous studies (Barstad and Nilssen 2012, 2015, 2016), the three *Pontania* species are shown to be highly adapted to the harsh environmental conditions in the Arctic.

Acknowledge

We are grateful for the field facilities provided by the “EcoFinn” project at The Arctic University of Norway, and the language improvement made by Robert T. Barrett at Tromsø University Museum. The study was funded by Tromsø University Museum.

References

- Barstad TE, Nilssen AC (2012) Hibernation adaptation and eclosion synchrony in leaf-galling sawflies in subarctic Norway. *Polar Biol* 35:1097-1103
- Barstad TE, Nilssen AC (2015) Spring phenology and the response to global warming in gall-inducing sawflies. *Polar Biol* 38:1503-1513
- Barstad TE, Nilssen AC (2016) Phenology during pre-diapause in gall-inducing sawflies and the influence of night length. Manuscript.
- Carr TG, Roininen H, Price PW (1998) Oviposition preference and larval performance of *Nematus oligospilus* (Hymenoptera: Tenthredinidae) in relation to host plant vigor. *Popul Ecol* 27:615-625
- Clancy KM, Price PW (1986) Temporal Variation in three-trophic-level interactions among willows, sawflies, and parasites. *Ecology* 67:1601-1607
- Cornelissen T, Fernandes GW, Vasconcellos-Neto J (2008) Size does matter: variation in herbivory between and within plants and the plant vigor hypothesis. *Oikos* 117:1121-1130
- Craig TP, Itami JK, Price PW (1989) A strong relationship between oviposition preference and larval performance in a shoot-galling sawfly. *Ecology* 70:1691-1699

- Craig TP, Itami JK, Price PW (1990) The window of vulnerability of a shoot-galling sawfly to attack by a parasitoid. *Ecology* 71:1471-1482
- Craig TP, Price PW, Itami JK (1986) Resource regulation by a stem-galling sawfly on the arroyo willow. *Ecology* 67:419-425
- Danks HV (1981) Arctic arthropods: a review of systematics and ecology with particular reference to the North American fauna. Entomol Soc Can, Ottawa
- Danks HV (1986) Insect plant interactions in Arctic regions. *Rev Entomol Quebec* 31:52-75
- Danks HV (1987) Insect dormancy: an ecological perspective. Biol Survey Canada, Natl Mus Nat Sci, Ottawa
- Danks HV (2004) Seasonal adaptations in Arctic insects. *Integr Comp Biol* 44:85-94
- Downes JA (1965) Adaptation of insects in the Arctic. *Annu Rev Entomol* 10:257-274
- Hanhimäki S, Senn J, Haukioja E (1995) The convergence in growth of foliage-chewing insect species on individual mountain birch trees. *J Anim Ecol* 64:543-552
- Henden JA, Ims RA, Yoccoz NG, Sorensen R, Killengreen ST (2011) Population dynamics of tundra voles in relation to configuration of willow thickets in southern Arctic tundra. *Polar Biol* 34:533-540
- Hjältén J, Roininen H, Danell K, Price PW (2003) Distribution and oviposition preference of galling sawflies in Arctic Canada. *Polar Biol* 26:768-773
- Humble LM (2006) Overwintering adaptation in arctic sawflies (Hymenoptera: Tenthredinidae) and their parasitoids: cold tolerance. *Can Entomol* 138:59-71
- Hunter AF (2000) Gregariousness and repellent defences in the survival of phytophagous insects. *Oikos* 91:213-224
- Hunter AF, Elkinton JS (2000) Effects of synchrony with host plant on populations of a spring-feeding Lepidopteran. *Ecology* 81:1248-1261
- Knerer G (1993) Life history diversity in sawflies. In: Wagner MR, Raffa KF (eds) Sawfly life history adaptations to woody plants. Academic Press Inc., San Diego, pp 33-59
- Kopelke J-P (1985a) Biologie und parasiten der gallenbildenden blattwespe *Pontania proxima* (Lepeletier 1823). *Senckenbergiana biol* 65:215-239
- Kopelke J-P (1985b) Über die biologie und parasiten der gallenbildenden blattwespenarten *Pontania dolichura* (THOMS. 1871), *P. vesicator* (BREMI

- 1849) und *P. viminalis* (L. 1758) (Hymenoptera: Tenthredinidae). Faun -Ökol Mitt 5:331-344
- Kopelke J-P (1991) Die arten der *viminalis*-gruppe, gattung *Pontania* O. Costa 1859, Mittel- und Nordeuropas (Insecta: Hymenoptera: Tenthredinidae). Senckenbergiana biol 71:65-128
- Kopelke J-P (1994) Der schmarotzerkomplex (brutparasiten und parasitoide) der gallenbildenden *Pontania*-arten (Insecta: Hymenoptera: Tenthredinidae). Senckenbergiana biol 73:83-133
- Kopelke J-P (1999) Gallenerzeugende Blattwespen Europas – Taxonomische Grundlagen, Biologie und Ökologie (Tenthredinidae: Nematinae: *Euura*, *Phyllocolpa*, *Pontania*). Cour Forsch Senck 212:1-183
- Kopelke J-P (2003) Natural enemies of gall-forming sawflies on willows (*Salix* spp.) (Hymenoptera: Tenthredinidae: *Euura*, *Phyllocolpa*, *Pontania*). Entomol Gen 26:277-312
- Kukal O, Kevan P (1987) The influence of parasitism on the life history of a high arctic insect, *Gynaephora groenlandica* (Wöcke) (Lepidoptera: Lymantriidae). Can J Zool 65:156-163
- Martel J, Kause A (2002) The phenological window of opportunity for early-season birch sawflies. Ecol Entomol 27:302-307
- McGeoch MA, Price PW (2004) Spatial abundance structures in an assemblage of gall-forming sawflies. J Anim Ecol 73:506-516
- Miller K, Werner R (1980) Supercooling to -60°C : an extreme example of freezing avoidance in northern willow gall insects. Cryobiology 17:621-622
- Mopper S (2005) Phenology-how time creates spatial structure in endophagous insect populations. Ann Zool Fennici 42:327-333
- Nyman T, Leppänen SA, Várkonyi G, Shaw MR, Koivisto R, Barstad TE, Vikberg V, Roininen H (2015) Determinants of parasitoid communities of willow-galling sawflies: habitat overrides physiology, host plant and space. Mol Ecol 24:5059-5074
- Price P, Craig TP (1984) Life history, phenology, and survivorship of stem-galling sawfly, *Euura lasiolepis* (Hymenoptera: Tenthredinidae), on the arroyo willow, *Salix lasiolepis*, in northern Arizona. Ann Entomol Soc Am 77:712-719

- Price P, Pschorn-Walcher H (1988) Are galling insects better protected against parasitoids than exposed feeders? a test using tenthredinid sawflies. *Ecol Entomol* 13:195-205
- Price PW (1991) The plant vigor hypothesis and herbivore attack. *Oikos* 62:244-251
- Price PW (1994) Phylogenetic constraints, adaptive syndromes, and emergent properties: from individual to population dynamics. *Res Popul Ecol* 36:3-14
- Price PW (2003) Macroevolutionary theory on macroecological patterns. Cambridge University Press, Cambridge
- Price PW, Carr TG (1986) Multiple effects of precipitation on *Salix lasiolepis* and populations of the stem-galling sawfly, *Euura lasiolepis*. *Ecol Res* 1:1-14
- Price PW, Carr TG (2000) Comparative ecology of membracids and tenthredinids in a macroevolutionary context. *Evol Ecol Res* 2:645-665
- Price PW, Clancy KM, Roininen H (1994) Comparative population dynamics of the galling sawflies. In: Price PW, Matteson WJ, Baranchikov YN (eds) Ecology and evolution of gall-forming insects. USDA For Serv N Central For Expt Stat Gen Tech Rep NC 174, pp 1-11
- Price PW, Ohgushi T, Roininen H, Ishihara M, Craig TP, Tahvanainen J, Ferrier SM (2004) Release of phylogenetic constraints through low resource heterogeneity: the case of gall-inducing sawflies. *Ecol Entomol* 29:467-481
- Price PW, Roininen H, Tahvanainen J (1987a) Plant age and attack by the bud galler, *Euura mucronata*. *Oecologia* 73:334-337
- Price PW, Roininen H, Tahvanainen J (1987b) Why does the bud-galling sawfly, *Euura mucronata*, attack long shoots. *Oecologia* 74:1-6
- Price PW, Roininen H, Tahvanainen J (1997) Willow tree shoot module length and the attack and survival pattern of a shoot-galling sawfly, *Euura atra* (Hymenoptera: Tenthredinidae). *Entomol Fennica* 8:113-119
- Quiring D, Flaherty L, Johns R, Morrison A (2006) Variable effect of plant module size on abundance and performance of galling insects. In: Ozaki K, Yukawa J, Ohgushi T, Price PW (eds) Galling arthropods and their associates. Springer-Verlag, Tokyo, pp 189-197
- Ring RA, Tesar D (1981) Adaptation to cold in Canadian Arctic insects. *Cryobiology* 18:199-211

- Roininen H (1991) Temporal change in the location of egg-laying by a bud-galling sawfly, *Euura mucronata*, on growing shoots of *Salix cinerea*. *Oecologia* 87:265-269
- Roininen H, Danell K (1997) Mortality factors and resource use of the bud-galling sawfly, *Euura mucronata* (Hartig), on willows (*Salix* spp.) in Arctic Eurasia. *Polar Biol* 18:325-330
- Roininen H, Danell K, Zinovjev A, Vikberg V, Virtanen R (2002) Community structure, survival and mortality factors in Arctic populations of *Eupontania* leaf gallers. *Polar Biol* 25:605-611
- Roininen H, Nyman T, Zinovjev AG (2005) Biology, ecology, and evolution of gall-inducing sawflies (Hymenoptera: Tenthredinidae and Xyelidae). In: Raman A, Schafer SW, Withers TM (eds) *Biology, ecology and evolution of gall-inducing arthropods*. Science Publishers, Inc., New Hampshire, pp 467-494
- Roininen H, Price PW, Tahvanainen J (1988) Field test of resource regulation by the bud-galling sawfly, *Euura Mucronata*, on *Salix cinerea*. *Holarctic Ecol* 11:136-139
- Santos JC, Silveira FAO, Fernandes GW (2008) Long term oviposition preference and larval performance of *Schizomyia macrocapillata* (Diptera: Cecidomyiidae) on larger shoots of its host plant *Bauhinia brevipes* (Fabaceae). *Evol Ecol* 22:123-137
- Singer MC, Parmesan C (2010) Phenological asynchrony between herbivorous insects and their host: signal of climatic change or pre-existing adaptive strategy? *Phil Trans R Soc* 365:3161-3176
- Strathdee AT, Bale JS (1998) Life on the edge: insect ecology in Arctic environments. *Annu Rev Entomol* 43:85-106
- Tauber MJ, Tauber CA, Masaki S (1986) *Seasonal adaptations of insects*. Oxford University Press, New York
- Viitasaari M (2002) *Sawflies (Hymenoptera, Symphyta) Vol I: a review of the suborder, the Western Palearctic taxa of Xyeloidae and Pamphiliidae*. Tremex Press Ltd, Helsinki
- Vikberg V (1970) The genus *Pontania* O. Costa (Hym., Tenthredinidae) in the Kilpisjärvi district, Finnish Lapland. *Ann Ent Fenn* 36:10-24

- Virtanen R, Oksanen L, Razzhivin V (1999) Topographical and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. *Acta Bot Fenn* 167:29-83
- Volney WJ, Fleming RA (2000) Climatic change and impacts of boreal forest insects. *Agric Ecosyst Environ* 82:283-294
- Wagner MR, Raffa, Kenneth F. (1993) Sawfly lifehistory adaptations to woody plants. Academic Press Inc, San Diego
- Walker DA, Raynolds MK, Daniels FJA, Einarsson E, Elvebakk A, Gould WA, Katenin AE, Kholod SS, Markson CJ, Melnikov ES, Moskalenko NG, Talbot SS, Yurtsev BA (2005) The circumpolar Arctic vegetation map. *J Veg Sci* 16:267-282
- Zinovjev AG (1993) Subgenera and Palaearctic species groups of the genus *Pontania*, with notes on the taxonomy of some European species of the *viminalis*-group (Hymenoptera: Tenthredinidae). *Zoosyst Ross* 2:145-154
- Zinovjev AG (1998) Palearctic sawflies of the genus *Pontania* Costa (Hymenoptera: Tenthredinidae) and their host-plant specificity. In: Csóka G, Matteson WJ, Stone GN, Price PW (eds) *Biology of gall-inducing arthropods*. USDA For Serv N Central For Res Stat Gen Tech Rep NC 199, pp 204-225
- Zinovjev AG, Vikberg V (1999) The sawfly of the *Pontania crassispina*-group with a key for the genera of the subtribe Eurina (Hymenoptera: Tenthredinidae, Nematinae). *Entomol Scand* 30:281-298

Figures

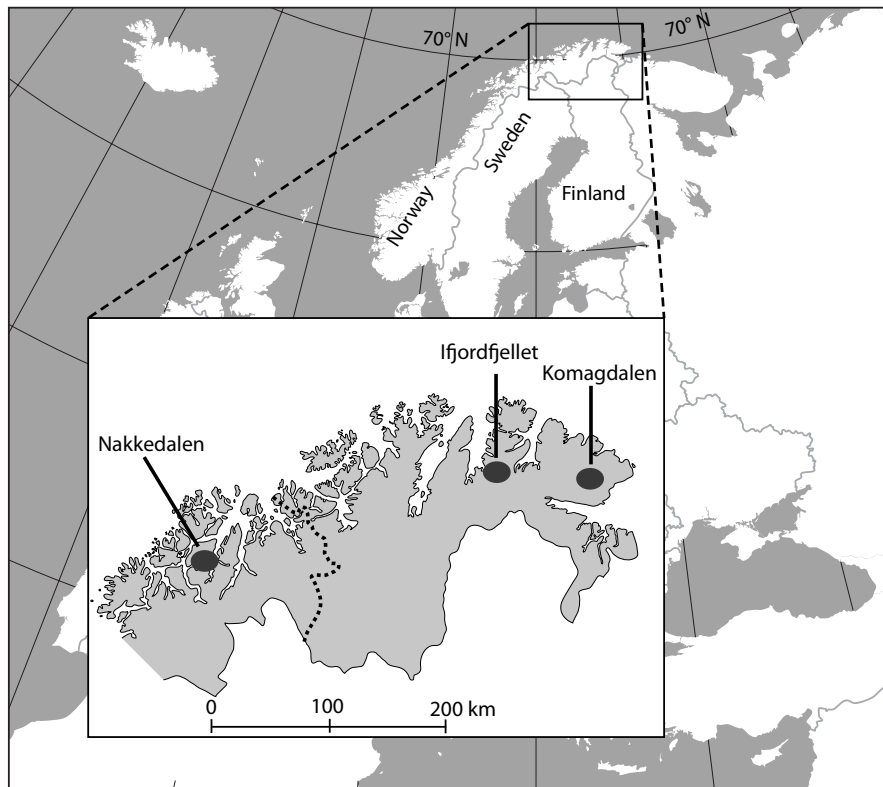


Fig. 1 The study sites in northern Norway, Komagdalen and Ifjordfjellet (70° N) and Nakkedalen (69° N).

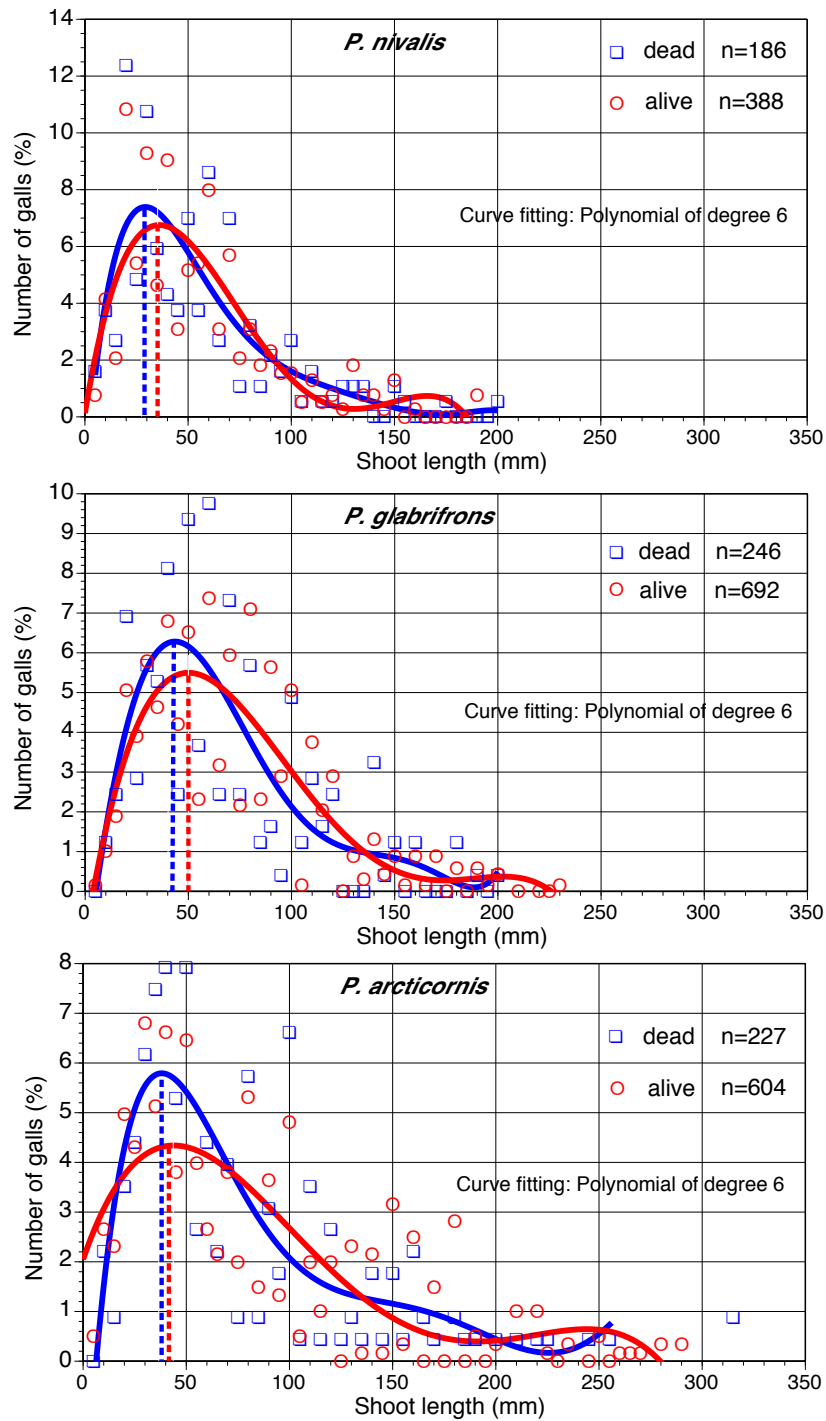


Fig. 2 Shoot length preferences and distribution of galls (%) in comparison between living and dead late stage larvae for *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*. The curves show that *P. nivalis* has an apex at a shoot length of 30-40 mm, whereas *P. glabrifrons* and *P. arcticornis* have an apex at 40-50 and 40 mm, respectively. *P. arcticornis* is able to utilize shoot lengths up to 250-300 mm. The curves of alive and dead stage larvae are very similar for all species.

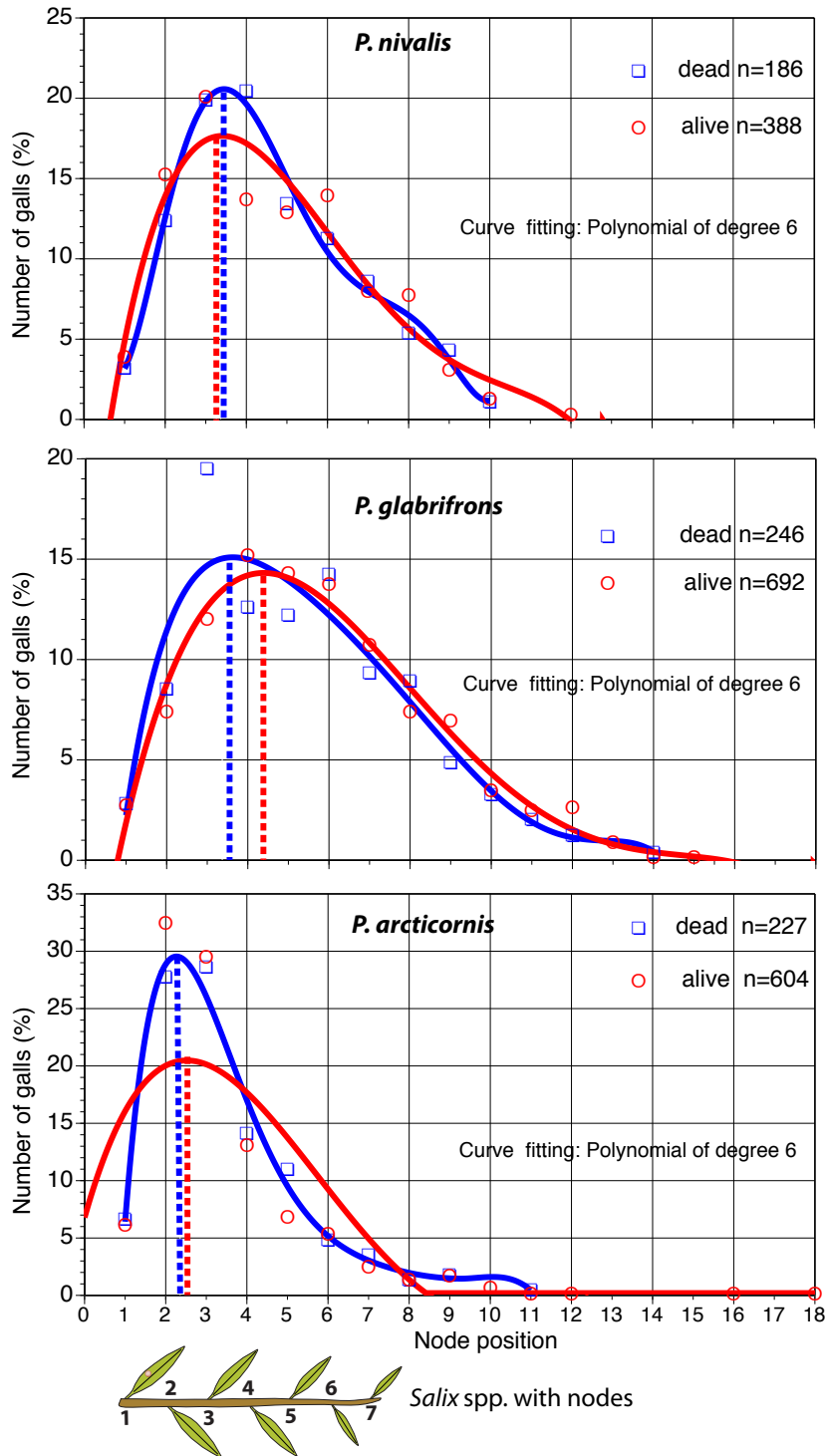


Fig. 3 Node position preferences and distribution of galls (%) in comparison between living and dead late stage larvae for *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*. As expected due to a high correlation between shoot length and node position, these graphs show the same trend as in Fig. 2, and the main point is that node position has no influence on survival of the larvae.

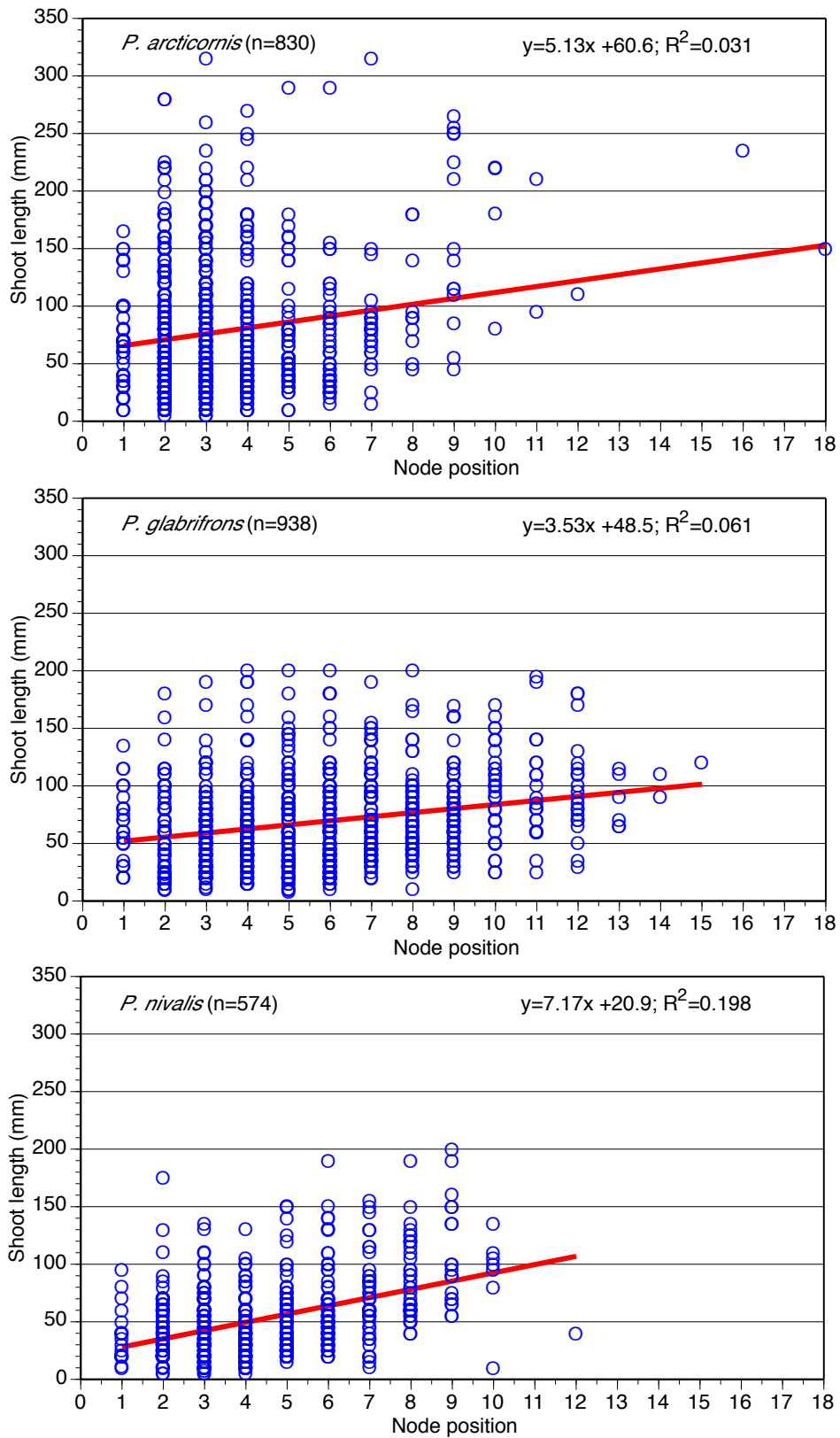


Fig. 4 Correlation between shoot length and node position preferences distribution of *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*.

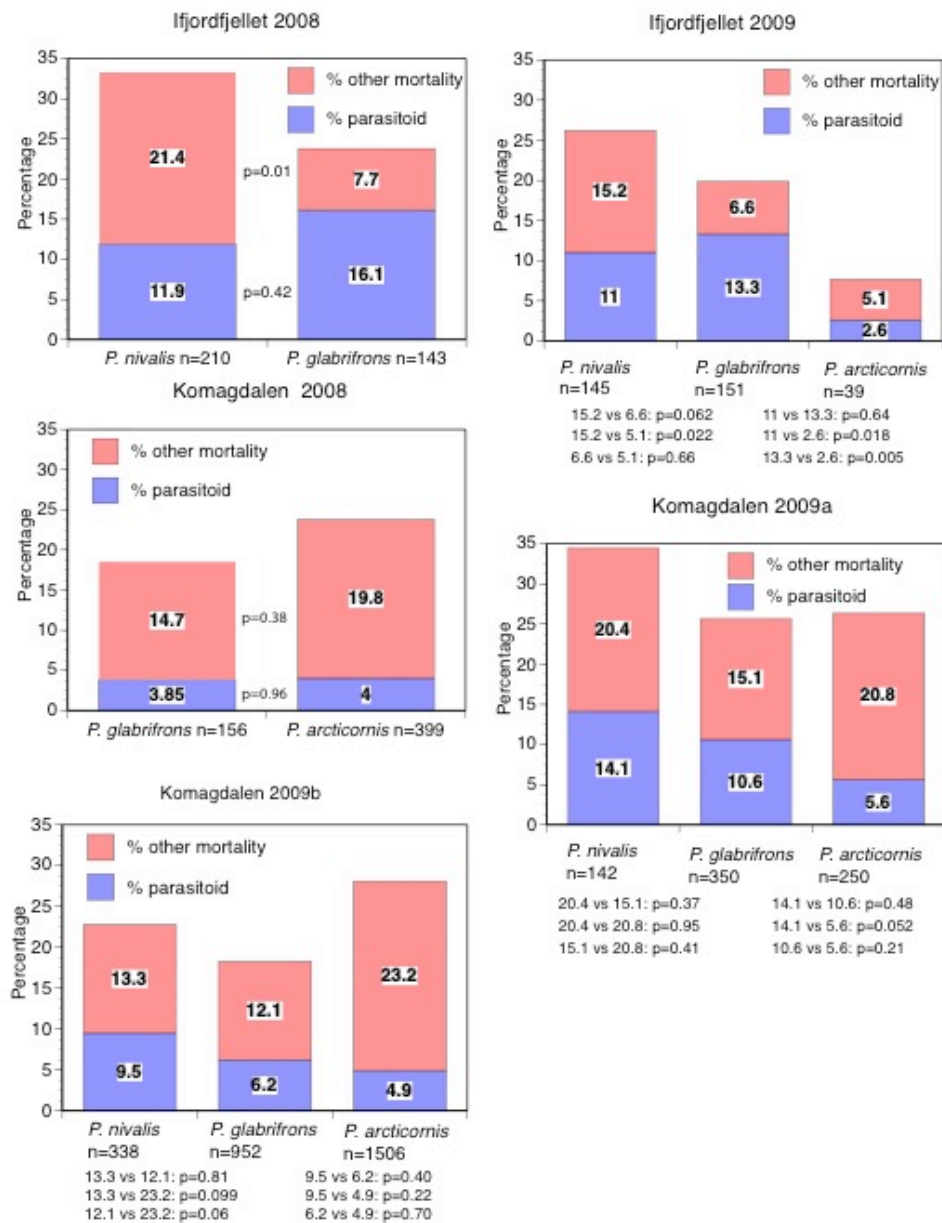


Fig. 5a Comparison in mortality factors, other mortality (%) and mortality caused by parasitoids (%) between the species *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*, within same site and year. Komagdalen 2009a and 2009b, show the two methods used to detect parasitoids (a = after pupation, parasitoid pupae, b = before pupation, parasitoid larvae). P-values from G-tests shown.

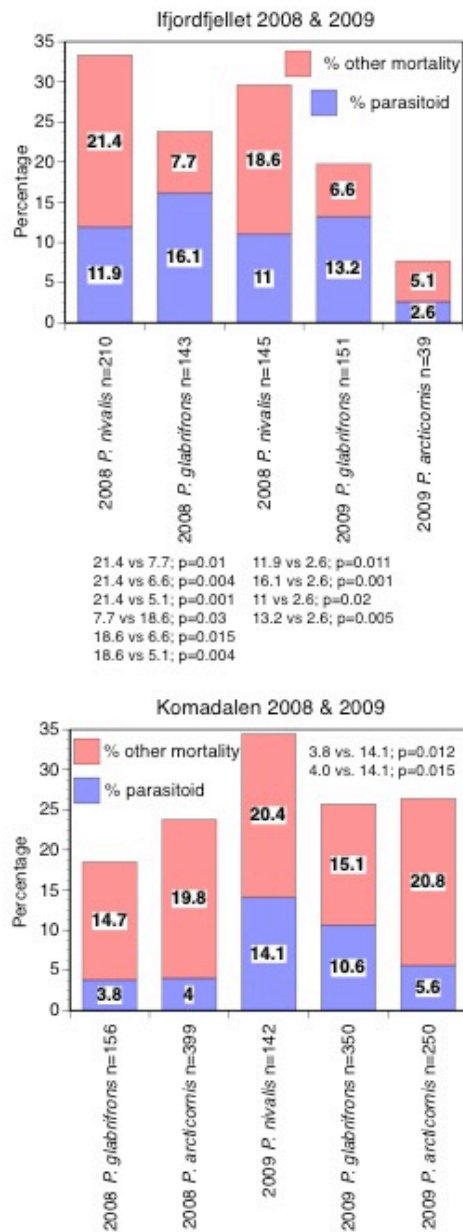


Fig. 5b Comparison in mortality factors, other mortality (%) and mortality caused by parasitoids (%), between species, *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*, and years (2008 and 2009), within the same sites (Ifjordfjellet and Komadalen). P-values from G-tests shown.

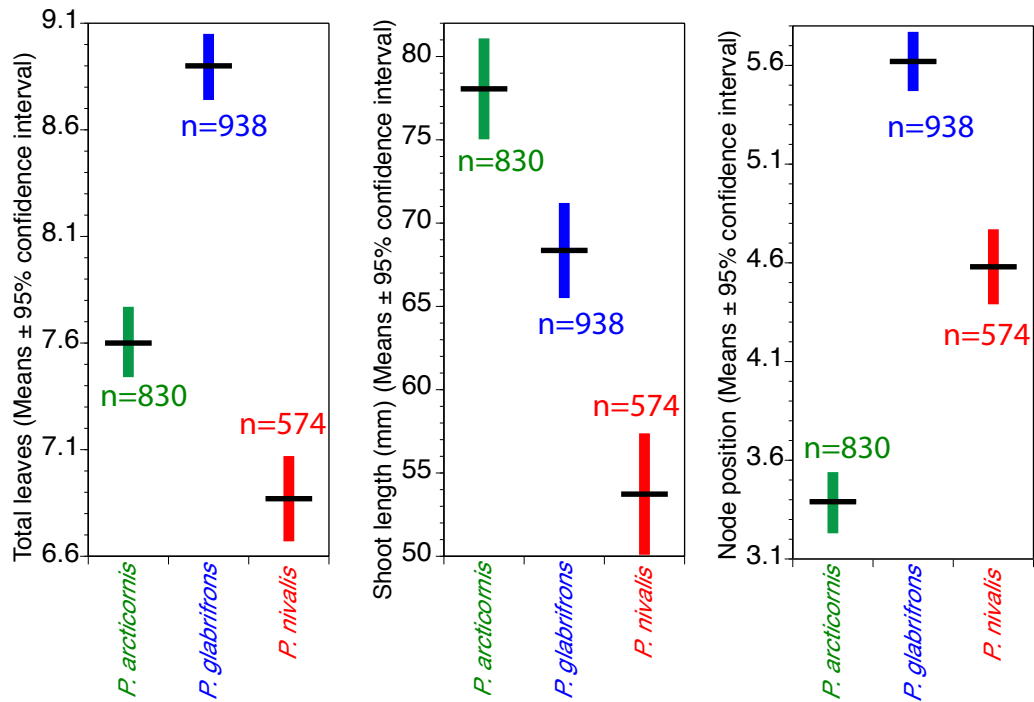
Supplementary tables and figures:

Supplementary Tab. 1 Larval survival rate for *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*, study sites and years (NA = Nakkedalen, 2012 and 2013, IF = Ifjordfjellet and KO = Komagdalen, 2008 and 2009). Sample size (total n = 2342, number of galls collected), observed larval activity (i.e. emergence holes in gall) (total n = 1684) and % larval survival (71.9 %). No data on *P. arcticornis*, IF 2008 and *P. nivalis*, KO 2008.

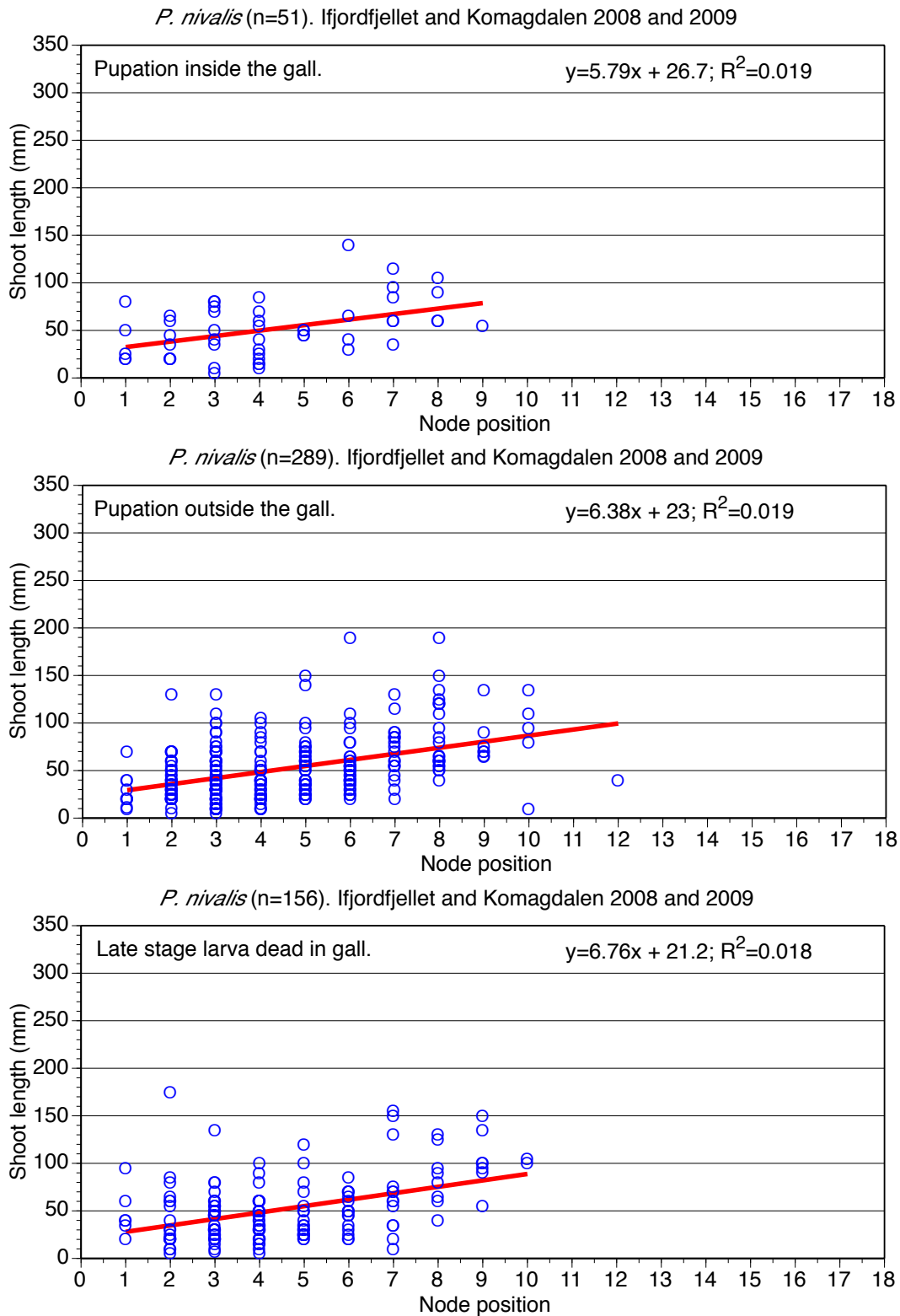
Species and study site	Sample size	Observed larvae activity	% larval survival
<i>Pontania nivalis</i> 2008 IF	210	140	66.7
<i>Pontania glabrifrons</i> 2008 IF	143	89	62.2
<i>Pontania arcticornis</i> 2008 IF	na		
<i>Pontania nivalis</i> 2009 IF	145	107	73.8
<i>Pontania glabrifrons</i> 2009 IF	151	121	80.1
<i>Pontania arcticornis</i> 2009 IF	39	35	89.7
<i>Pontania nivalis</i> 2008 KO	na		
<i>Pontania glabrifrons</i> 2008 KO	156	127	81.4
<i>Pontania arcticornis</i> 2008 KO	399	304	76.2
<i>Pontania nivalis</i> 2009 KO	142	93	65.5
<i>Pontania glabrifrons</i> 2009 KO	350	260	74.3
<i>Pontania arcticornis</i> 2009 KO	250	183	73.2
<i>Pontania nivalis</i> 2012 NA	60	38	63.3
<i>Pontania glabrifrons</i> 2012 NA	50	27	54.0
<i>Pontania arcticornis</i> 2012 NA	53	16	30.2
<i>Pontania nivalis</i> 2013 NA	17	10	58.8
<i>Pontania glabrifrons</i> 2013 NA	86	68	79.1
<i>Pontania arcticornis</i> 2013 NA	92	66	71.7

Supplementary Tab. 2 Mortality factors and pupation location for *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*, for Ifjordfjellet and Komagdalen, 2008 and 2009. If= Ifjordfjellet, KO=Komagdalen, 2009 KOa and 2009 KO b, show the two methods used to detect parasitoids (a = after pupation, parasitoid pupae, b = before pupation, parasitoid larvae). COD=cause of death, B=pupation outside gall and A=pupation inside gall.

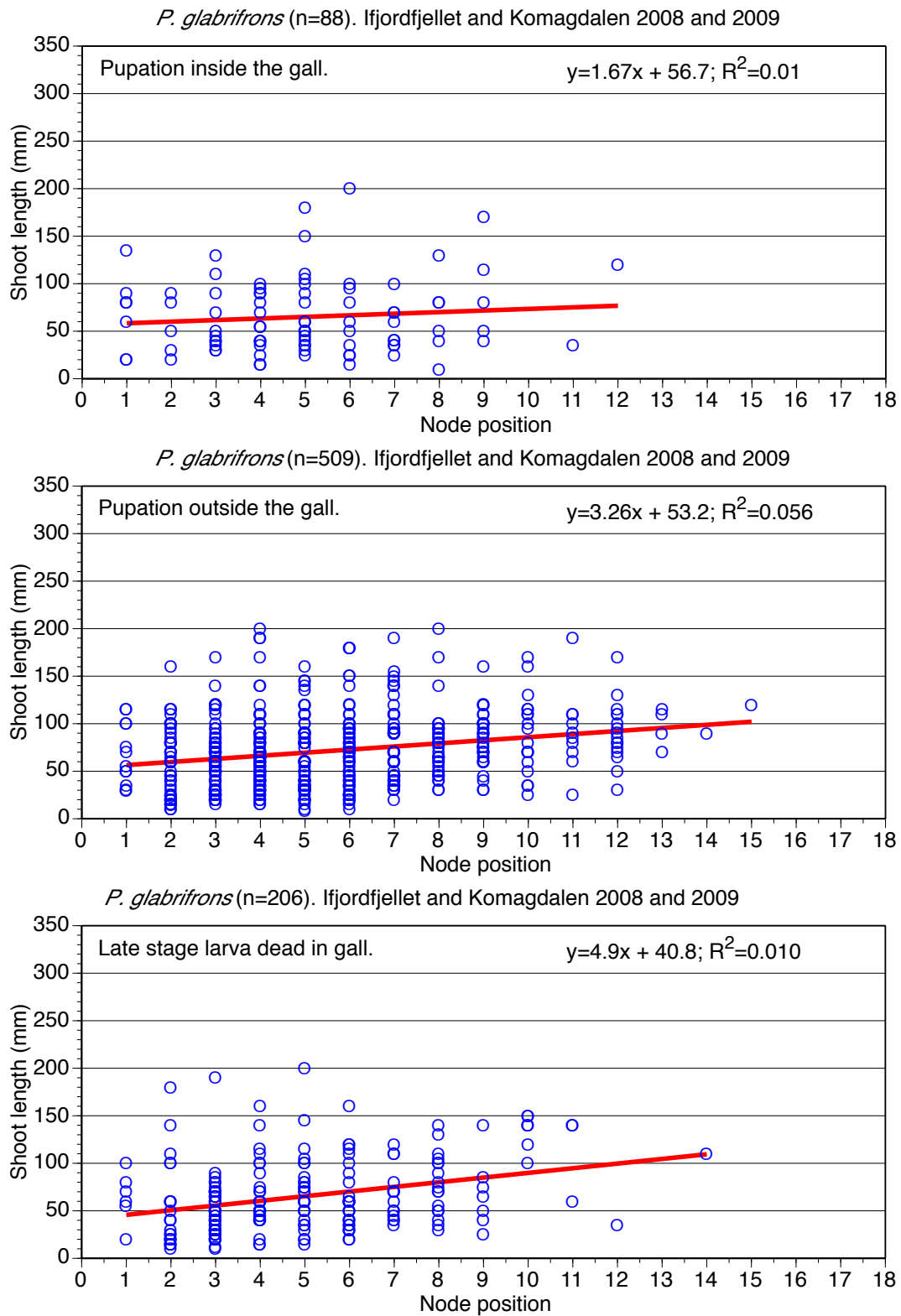
Species	Sample size	Mortality (%)	Parasitism (%)	COD unknown (%)	Pupae location (B/A)	% Pupae location A
<i>Pontania nivalis</i> 2008 IF	210	70 (33.3)	25 (11.9)	45 (21.4)	119/21	17.6
<i>Pontania nivalis</i> 2009 IF	145	38 (26.6)	16 (11.0)	27 (15.2)	93/14	15.1
<i>Pontania nivalis</i> 2008 KO	na					
<i>Pontania nivalis</i> 2009 KO (a)	142	49 (34.5)	20 (14.1)	29 (20.4)	77/16	20.8
<i>Pontania nivalis</i> 2009 KO (b)	338	77 (22.8)	32 (9.5)	45 (13.3)	na	
<i>Pontania glabrifrons</i> 2008 IF	143	34 (23.8)	23 (16.1)	11 (7.7)	78/11	14.1
<i>Pontania glabrifrons</i> 2009 IF	151	30 (19.9)	20 (13.2)	10 (6.7)	105/16	15.2
<i>Pontania glabrifrons</i> 2008 KO	156	29 (18.6)	6 (3.8)	23 (14.8)	105/22	21
<i>Pontania glabrifrons</i> 2009 KO (a)	350	90 (25.7)	37 (10.6)	53 (15.1)	221/39	17.6
<i>Pontania glabrifrons</i> 2009 KO (b)	952	174 (18.3)	59 (6.2)	115 (12.1)	na	
<i>Pontania arcticornis</i> 2008 IF	na					
<i>Pontania arcticornis</i> 2009 IF	39	3 (7.7)	1 (2.6)	2 (5.1)	33/2	6.1
<i>Pontania arcticornis</i> 2008 KO	399	95 (23.8)	16 (4.0)	79 (19.8)	288/16	5.6
<i>Pontania arcticornis</i> 2009 KO (a)	250	184 (26.4)	14 (5.6)	52 (20.8)	159/24	15.1
<i>Pontania arcticornis</i> 2009 KO (b)	1506	424 (28.2)	74 (4.9)	350 (23.2)	na	



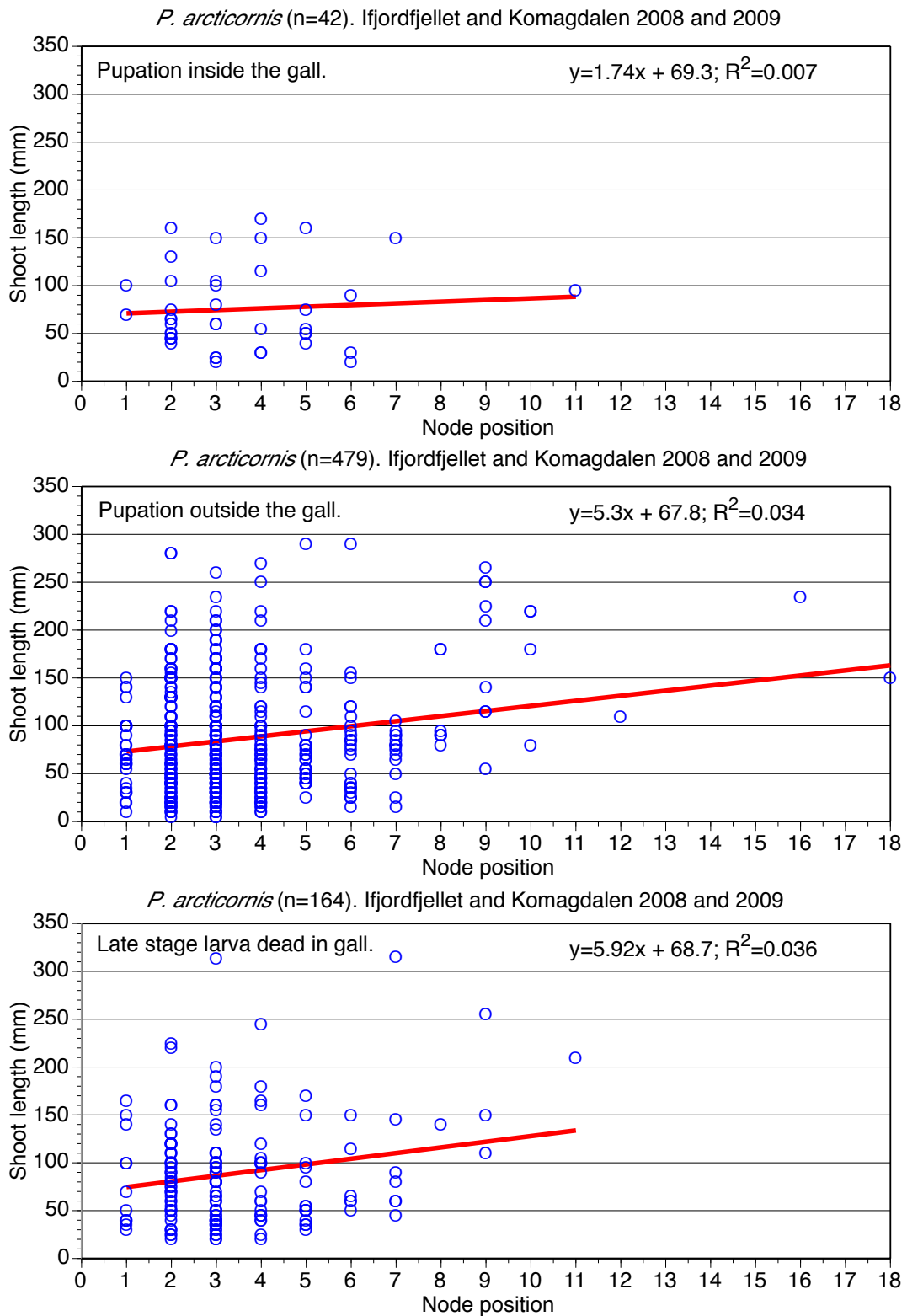
Supplementary Fig. 1 Willow host preferences in comparison between *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis*. Total leaves on shoots, shoot length with galls and node position of galls on shoots were the dependent variables, and species were factors in GENLIN-analyses in SPSS 23 with Distribution=Normal and Link=identity. The calculated means ± 95% confidence intervals were graphed. There are no overlap between the species, and consequently significant differences ($p < 0.005$) between all three species.



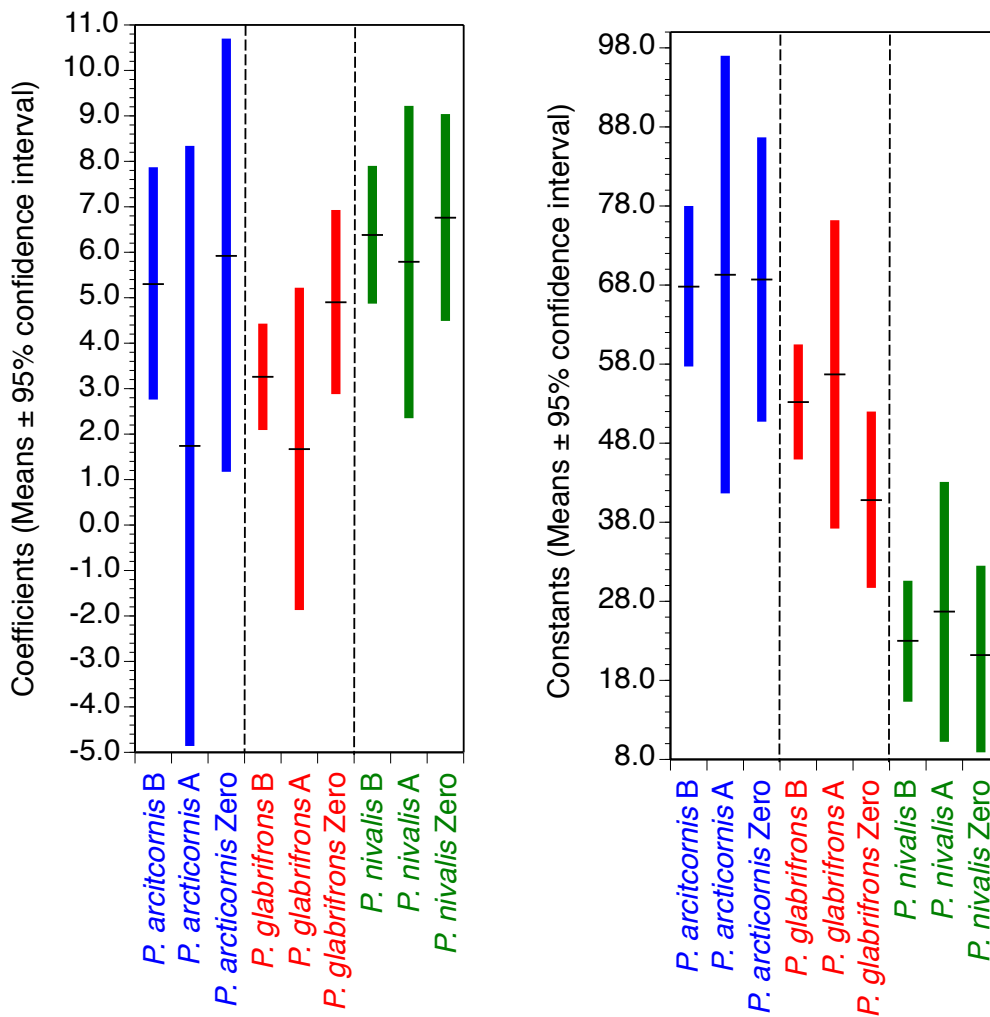
Supplementary Fig. 2a Correlation between shoot length and node position preferences distribution for *Pontania nivalis*. Figures show B=pupation outside gall, A=pupation inside gall and Zero=dead late stage larvae.



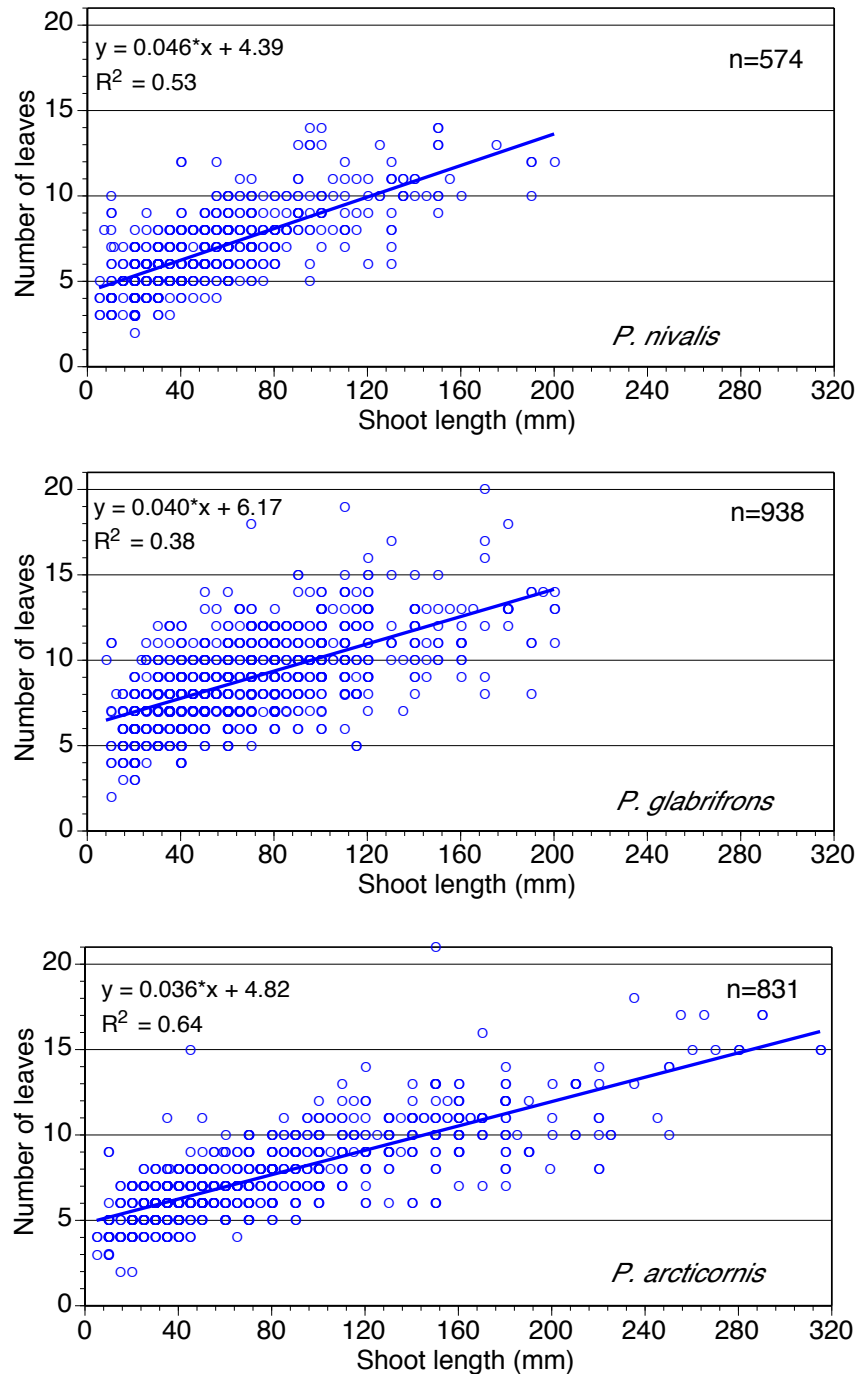
Supplementary Fig. 2b Correlation between shoot length and node position preferences distribution for *Pontania glabrifrons*. Figures show B=pupation outside gall, A=pupation inside gall and Zero=dead late stage larvae.



Supplementary Fig. 2c Correlation between shoot length and node position preferences distribution for *Pontania arcticornis*. Figures show B=pupation outside gall, A=pupation inside gall and Zero=dead late stage larvae.



Supplementary Fig. 3 Willow host preferences comparison between *Pontania nivalis*, *P. glabrifrons* and *P. arcticornis* from Ifjordfjellet and Komagdalen, 2008 and 2009. B=pupation outside gall, A=pupation inside gall and Zero=dead late stage larvae (means ± 95% confidence interval of coefficients and constants from the linear regressions given in Figs.3a, 3b and 3c).



Supplementary Fig. 4 Correlation between shoot lengths and number of leaves on shoots for the total material ($n=2343$; i.e. all years and all sites) collected of *Pontania nivalis* on *Salix glauca*, *P. glabrifrons* on *S. lanata* and *P. arcticornis* on *S. phylicifolia*. The coefficients are quite similar, but *P. arcticornis* is able to use longer shoot lengths than the two other species. Observe that overlapping values (rings) cannot be visualized in the graph.