Naoyuki Matsumoto · Tom Hsiang

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The Battle Under Snow Between Fungal Pathogens and Their Plant Hosts

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Preface

Climate change does not occur uniformly across the globe; its effects are considered most severe at higher latitudes in the northern hemisphere, and agricultural production is most likely to be influenced there (Murray and Gaudet 2013). This concern motivated scientists to convene an interdisciplinary forum, Plant and Microbe Adaptations to Cold (PMAC), in 1997 in Sapporo, Japan. Fifteen years later, PMAC 2012 met again in Sapporo, and this conference focused on sustainable agricultural production under changing climatic conditions. Scientists, as well as farmers and policy makers, participated the conference to discuss issues of importance affected by climate change. Although concrete countermeasures were not presented, available scientific knowledge and established techniques can be adapted to minimize overwintering problems of crops. For example, extended snow cover for up to 163 days in certain areas of Hokkaido in northern Japan in the 2011/2012 winter (S. Inoue, personal communication) made farmers anxious; however, the survival of winter wheat was better than expected.

Both biotic and abiotic factors that affect agricultural production respond to changes in winter climate. Abiotic factors mainly consist of freeze damage due to low temperatures and of ice encasement and damage that occur after repeated cycles of freezing and thawing of soil. Biotic factors are comprised mostly of snow molds incited by low-temperature fungi that prevail on plants under snow cover and represent the main theme of this book.

Winter damage to agricultural production, unlike drought in summer, is not well documented. Gudleifsson (2013) presented an example in Iceland, where analyses of ice cores from glaciers indicated that the temperatures around the time of settlement from 900 to 1200 were fairly high and then fluctuated until 1900 with frequent winter damage to forage grass. Over one-third of the years were characterized as having mild or severe winter damage of pastures, resulting in reduced livestock production and subsequent famine. Correlations between temperature measurements and hay yield from 1900 to 2010 revealed that winter temperatures affected forage production more significantly (r=0.57***) than summer temperatures (r=0.28***). Recent global warming is generally considered to favor forage production.

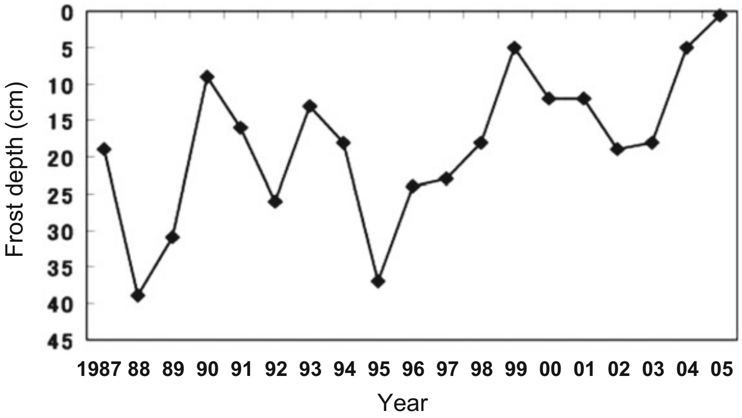

Fig. 1 Change in annual soil frost in nine spots in Memuro, Hokkaido (Hirota et al. 2006)

Climate change also affects agriculture in Hokkaido, Japan, where the quantity and quality of summer crops have been improved due to extended growth periods and increased cropping acreage, as well as reduced cool weather damage. The trends are not so apparent in forage crops or winter wheat that overwinters under snow. However, especially in eastern Hokkaido where deep soil frost is characteristic of the winter climate, early onset of snow cover and deep snow cover has attenuated the depth and duration of soil frost (Fig. 1, Hirota et al. 2013). Consequently, changes in winter climate have led to changes in snow mold flora, affecting breeding strategy.

In this book, we described a common phenomenon occurring in snowy regions, namely, snow mold. Snow mold is important not only as one of agricultural issues in cold regions but interesting as a biological phenomenon. This book is an English version of the book *Snow Mold* written in Japanese by NM (Matsumoto 2013) and represents a synthesis of ideas of both authors of this version.

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Contents

Chapter 1
Introduction

Abstract In cold-temperate region, plants are more frequently damaged by biotic factors, primarily snow mold, than by abiotic factors such as freezing. Snow mold is used here as a generic name for plant diseases that occur under snow cover. Many different fungi may be involved, and each snow mold fungus has its own ecological and physiological features. They normally infect and can prevail on plants under snow, but generally are dormant during other seasons. Their habitat under snow is characterized by constant low temperature, darkness, and high moisture. Snow mold fungi are, in general, opportunistic pathogens, which, in the absence of antagonists, attack plants depleted of reserve material. Such organisms which not only tolerate cold temperatures but thrive under such conditions are called "psychrophiles." In the final section of this chapter, ambiguities in the use of the common term "psychrophile" are illustrated, and these are ascribed to the complex life cycles of different fungi. Another term, "cryophile," may be more appropriate, to denote fungi, including snow mold fungi that prevail in the cryosphere.

Dr. Takao Araki who showed NM the significance of field observations and led him to a whole new world under snow; photograph taken circa 1978.

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In cold-temperate region, agricultural fields are often covered with snow for more than 4 months, and plant tops look dormant even before snow cover and are yellowed after snow cover. From the point of view of the plant, half of the year is winter. However, despite harsh winter climates in such regions, plant growth is promoted due to longer day lengths in summer. Survival through winter months is the greatest challenge for such organisms. Wild plants have consequently developed diverse winter survival strategies (Sakai 2003). Overwintering domesticated plants such as winter cereals and forage crop have been selected and protected by humans, resulting in yield increases. Today, we are facing another difficulty, namely, global warming.

1.1 Snow Mold

In the temperate region, plants are more likely to be killed by snow mold (a biotic factor) than freezing or ice encasement (abiotic factors). We are generally unable to observe the process of pathogenesis under snow, but can see the consequences after snowmelt. Snow mold damage becomes evident by a delay in plant growth or by outright plant death. Frequently, disease surveys have been made in northern hemisphere countries on overwintering crops, e.g., cereals and forage crops in Idaho, USA, by Remsberg and Hugerford (1933); forage crops in Alaska, USA, by Lebeau and Logsdon (1958); winter wheat (*Triticum aestivum*) in Ontario, Canada, by Schneider and Seaman (1987); turfgrass in Alberta, Canada, by Vaartnou and Elliott (1969); winter cereals in Alberta, Canada, by Gaudet and Bhalla (1988); forage crops and winter cereals in Saskatchewan, Canada, by Smith (1975); winter cereals in Saskatchewan, Canada, by Gossen and Reiter (1989); forage crops in northern Finland by Mäkelä (1981); forage crops in Norway by Årsvoll (1973); forage crops in northern Norway by Andersen (1992); and forage crops in Iceland by Kristinsson and Gudleifsson (1976). These surveys documented the fungi *Sclerotina borealis*, *Typhula ishikariensis*, *T. incarnata*, and *Microdochium nivale* as important snow mold pathogens. Smith (1975) emphasized the need for more detailed studies on these pathogens in terms of environmental factors and disease incidence.

Plants are seldom killed during overwintering with a few exceptions (Hakamata et al. 1978, Fig. 1.1). In regions of long severe winters, plants have been naturally or artificially selected for winter hardiness and survival at the expense of productivity. Plants often look dead just after snowmelt, but soon resume growth because the crowns have remained alive (Fig. 1.2). Phenomena referred to as “winter kill” or “winter damage” may have biotic or abiotic sources, but sometimes the causal agent remains unidentified or may be obscure. “Winter kill” and “winter damage” in certain regions are mostly caused by snow mold. Using 12 orchardgrass cultivars, Abe and Matsumoto (1981) analyzed factors involved in their overwintering in

Fig. 1.1 Freezing damage on perennial ryegrass planted in a square in Løken, Norway. Timothy surrounding the perennial ryegrass plot survived and remained green. The field was located on a slope where ice encasement was unlikely to occur

Fig. 1.2 Turfgrass damage in a golf course nursery induced by *Typhula ishikariensis*. Fungicide applications prior to snow cover protected plants from damage, and the plants greened up quickly after snow melt (*left-side* plot). Leaves were killed, but later green shoots appear indicating that crowns and roots were not also entirely killed (*right-side* plot)

Table 1.1 Major snow molds on agricultural crops[a]

Disease	Taxonomic position		Scientific name
	Chromalveolata		
		Oomycota	
Snow rot			*Pythium iwayamai*
			P. okanoganense
			P. paddicum
	Fungi		
		Ascomycota	
Pink snow mold			*Microdochium nivale*
Sclerotinia snow mold			*Sclerotinia borealis*
Snow mold			*S. nivalis*
Clover rot			*S. trifoliorum*
Supponuke disease		Basidiomycota	*Athelia* sp[b]
Cottony snow mold			*Coprinus psychromorbidus*
Gray snow mold			*Typhula incarnata*
Speckled snow mold			*T. ishikariensis*

[a]Snow molds on forest trees are excluded
[b]Inferred from rDNA ITS sequence (A. Kawakami, personal communication)

Sapporo, Hokkaido, Japan, to reveal that the resistance to *Typhula* spp. was the most important survival factor.

Snow mold is a generic term referring to diseases that are incited by fungal pathogens prevailing under snow, and it does not indicate a specific taxonomic group of fungi (Table 1.1). Many ascomycetes and basidiomycetes are known as snow mold pathogens. Oomycetes, which are not fungi but belong to Chromalveolata, can also cause snow mold. Zygomycetes or Chytridiomycetes have not been identified as snow mold pathogens so far but need critical examination.

1.1.1 Damage

Several fungal species are known to attack plants under snow. They are divided into two types: ones occurring regularly year after year and the others irregularly (Nissinen 1996). The occurrence of the latter type is unpredictable, and specific winter climate conditions favor their outbreak. *Sclerotinia borealis* caused serious damage to orchardgrass in 1975 in eastern Hokkaido, and farmers resorted to importing feedstuff from abroad (Araki 1975). Of 15,000 ha of grasslands in this area, 62 % required reseeding, 28 % needed renewal, and 10 % were planted with other crops. The outbreak of *Sclerotinia* snow mold is ascribed to the two climatic factors in the winter of 1974/1975: (i) delayed onset of snow cover predisposing orchardgrass to disease with low-temperature stress and (ii) deep snow cover in late March prolonging thaw and