**Puccinia subnitens**: An Obscure Rust Pathogen
Little-Known for More than a Century

Robert M. Harveson, Panhandle Research and Extension Center, University of Nebraska-Lincoln, Scottsbluff 69361

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**ABSTRACT**

Sugar beet seedling rust, caused by *Puccinia subnitens*, is a rarely occurring but essentially harmless disease in sugar beet production. However, it has caused substantial but sporadic losses to commercial spinach growers. It has the typically complex life cycle of a macrocyclic rust pathogen, but is also unusual because it is one of the few documented heteroecious rust diseases where the early spore stages (pycnial and aecial) occur on the economic host while the normally damaging, repeating, uredial stage is found on the feral, noneconomic host. Most significantly, it was one of the first heteroecious rust diseases recognized to have the ability to infect numerous, distinct host species with the aecial stage while maintaining a relatively narrow host range for its uredial and telial stages.

**INTRODUCTION**
In May of 2009, an obscure and rarely occurring rust disease, sugar beet seedling rust, caused by *Puccinia subnitens*, was identified on young sugar beet plants in the western Nebraska Panhandle. The incidence in the field where it was first discovered was high enough (25%) to cause concern by the grower, but after investigating the identity and life history of the pathogen, it was happily concluded that no economic damage would result from the infection. Having gained this knowledge from the study, the producer was able to avoid unnecessary fungicide applications. Similarly, the information in this report would also be of use to others who might encounter the disease in the future.

*Puccinia subnitens*, Dietel (syn. *P. aristidae* Tracy), is a macrocyclic pathogen that causes a heteroecious rust disease of Chenopodiaceous crops known as sugar beet seedling rust. Only the pycnial and aecial stages occur on the hosts of economic importance, sugar beet and spinach, while the other stages (uredial and telial) infect saltgrass (*Distichlis* spp.) and occasionally needlegrass (*Aristida* spp.) (13,21).

**PRIMARY HOST**
The major documented host for *P. subnitens* is the inland saltgrass (*Distichlis spicata* L. Greene) (8,11,12), a warm-season grass native to the Americas. Saltgrass is distributed widely across the North American continent, occurring commonly from Mexico north to the Northwest Territories, east to Maine, and south to Florida and the Gulf Coast of the United States. Along the Atlantic seaboard and the Gulf Coast of the United States, it is found primarily in coastal salt marsh communities. In the western United States, the plant occurs on the coast as well as inland, in brackish, marshy areas or high saline soils (11). The plant is very drought tolerant, flourishing happily in the strongly alkaline soils found throughout western North America and the Great Plains (11,12).

**PATHOGEN LIFE CYCLE, SIGNS, AND SYMPTOMS**
The pathogen life cycle (Fig. 1) is quite complex. Beginning in early spring, the overwintering teliospores germinate from telial pustules on the inland saltgrass to produce basidiospores, which then are spread by wind to a number of alternate hosts in multiple plant families; including sugar beets (see Early History of Disease below). The basidiospore infections give rise sequentially to the pycnial and aecial spore stages. Pycnial lesions are circular and light yellow, measuring 2-5 mm in diameter (Fig. 2a). Flask-shaped pycnia containing receptive hyphae and spermatia (Fig. 3) are found embedded within lesions and are generally located on the upper leaf surface (Fig. 4). The aecia are usually found on the lower leaf surface after developing directly from the pycnia following fertilization (Fig. 4). The aecial lesions consist of clusters of yellowish-orange, rounded structures (Figs. 2b and 5) that gradually become cup-shaped, releasing spores after...
rupturing (Fig. 6), and are distinctively found arranged in circular patterns (Fig. 7). As new aeciospores are formed, they reinfect the inland saltgrass, giving rise to new uredia and telia (14), thus completing the life cycle (Fig. 1).

**EARLY HISTORY OF DISEASE IN ALTERNATE HOSTS**

In 1895, Paul Dietel published the first description of *Puccinia subnitens* occurring on saltgrass specimens from Montana (7). Subsequently, numerous individuals recognized the fungus commonly infecting various *Distichlis* species across North America from the Atlantic to the Pacific Oceans. The Colorado-based educator and naturalist Ellsworth Bethel related his experiences, stating: “in the western states this grass (saltgrass) is almost always badly rusted. In fact, it would be rare to find even a small area where the rust is absent”(6).

A consistent and intimate association between *P. subnitens* infections on saltgrass and aecial rust infections on common lambsquarters (*Chenopodium album*) (Fig. 8) was also widely noted along the eastern seaboard, throughout the Great Plains and western United States, stretching from North Dakota and Montana to New Mexico and Arizona to California and Oregon on the Pacific coast (6).

The widespread area represented by these reports reflects a remarkable competency of the pathogen to apparently adapt to regions with highly variable environments. In arid regions of western North America, there is seldom sufficient precipitation to germinate all teliospores at once. Teliospores found on dead leaves lying on the ground tend to germinate first while those spores residing in pustules infecting leaves of live plants will germinate at a later time, still remaining viable until late summer (5,6). This pathogen has further established the ability to advantageously produce a new crop of aecia following each period of abundant moisture throughout the summer (5,6).
The Reverend John Mallory Bates and Ellsworth Bethel, residents of Nebraska and Colorado, respectively, were two highly significant but currently little-known figures in American mycology, both of whom were instrumental in elucidating the life cycle, pathology, and host range of *P. subnitens* early in the 20th century. Their prescient observations contributed greatly to our current knowledge of this rust pathogen through their cooperation and collaborations with other scientists, in particular the noted rust pathologist John C. Arthur. They both freely shared their notes and specimens with others, often unselfishly shunning the opportunity to publish results themselves. Neither was formally trained in botany or mycology, but were both self-taught, studying fungi as a hobby.

**BATES AND BETHEL: EARLY AMATEUR MYCOLOGISTS**

Before 1904, common lambsquarters (*C. album*) was the only known aecial host for this rust pathogen. However, in the summer of 1904, John Mallory Bates postulated that aecia he observed in Nebraska infecting species of *Cleome* (Beeweed), *Sophia* (tansymustard), *Lepidium* (pepperweed), *Erysimum* (wallflower), and *Salsola* (Russian thistle) were all related to *P. subnitens* (2,5). Bates was an Episcopalian clergyman widely known and respected in his day as an amateur naturalist and botanist. Bates related his observations to J. C. Arthur and sent him teliospores from *Distichlis*, in addition to infected seedlings of *Cleome serrulata* and *C. album* covered profusely with the yellowish-orange-colored aecia. Bates also sent Arthur freshly collected specimens later that year containing aecia on *Roripa sinulata* (spreading yellowcress), *Sophia incisa*, and *Salsola tragus* that he also presumed to belong to the same rust species. Arthur concluded that the aecia from these plants were identical to *P. subnitens* and also confirmed Bates’ deductions by growing the teliospores on these same plant hosts and detecting the formation of new aecia (2). Arthur considered it noteworthy that *P. subnitens* was capable of infecting this number and diversity of host plants. This discovery proved to be a watershed concept, shattering the previously held paradigms involving rust investigations at that time (2,3).

**BETHEL’S EXPERIENCES WITH AECIAL HOSTS OF *P. SUBNITENS IN COLORADO***

Bethel, much like Bates in Nebraska, became well known as an extraordinary collector and authority on the rust flora of Colorado and other areas of the southwestern United States. He repeatedly demonstrated that *P. subnitens* had many of the same aecial host species distributed throughout Colorado as those of Bates’ observations in Nebraska. He further verified these assumptions of relatedness by growing the fungus on various plants in his home garden, which eventually became an open-air laboratory for this and many other rust species.

His collaborative spirit and enthusiasm was exhibited by his frequent role as a host for visiting scientists on regional rust collection trips. After participating in collection surveys with Bethel in the Denver, Colorado area in 1916, J. C. Arthur remarked that “this region is the richest and most varied known to the writer and resulted in large increases in knowledge pertaining to new forms and combinations” (3). By 1934, the combined works of Bates, Bethel, Arthur, and others further confirmed and expanded the host range of *P. subnitens* to include an amazing
total of at least 100 species from 24 families representing more than 50 genera (1, 2, 3, 5, 6).

**SUGAR BEET SEEDLING DISEASE**

Although it has been readily demonstrated that the aecial form of *P. subniten*s is often found on many disparate weed and ornamental species, infection on cultivated, economic host plants is restricted to members of the Chenopodiaceae, including sugar beet, mangel, Swiss chard, and spinach (2, 20, 21). The first published report of this disease on sugar beets was by Pool and McKay in 1914 from Colorado (15). They found the rust occurring frequently during the 1912-1913 seasons from multiple fields in the Arkansas Valley near Rocky Ford in southeast Colorado. During May and June, the pathogen produced aecial lesions that were primarily restricted to the young sugar beet cotyledons. They also mentioned moderate damage occurring on infected beet crowns. Pool and McKay further noted the presence of lambsquarters heavily infected with aecial lesions from the same general locations. By early July, the disease intensity and severity had been reduced to the point where it was no longer considered an issue of concern. They also added that a telial form (presumed to be the same pathogen) was found abundantly colonizing saltgrass stands in the vicinity of sugar beet fields during the epidemics. This was followed by new uredia being identified in early June on saltgrass (15) before being converted back to telia in late July.

Pool and McKay (13) additionally mentioned that they learned from conversations with local agronomists that this disease had been seen only once before in Colorado. Correspondence with J. C. Arthur further revealed that his past experiences had confirmed the presence of the pathogen once before on sugar beets in the state, but the finding was apparently never published. They finally concluded that the disease was not severe during these two seasons, but that if conditions were more conducive, significant damage could be induced on young plants due to the profusion of infected saltgrass stands within close proximity of sugar beet fields (15).

**NEW REPORT FROM NEBRASKA**

In mid-May 2009, young sugar beet plants were first observed exhibiting signs suggestive of sugar beet seedling rust in a field near Bayard, Nebraska (Fig. 9), after an extended period of unusually cool and wet weather had persisted throughout the western Nebraska Panhandle in April and early May (9). Pycnial lesions were circular and yellowish, 2-5 mm in diameter (Fig. 2a), containing flask-shaped pycnia (Fig. 3) as described above, with globose, verrucose aeciospores measuring approximately 17-22 µm × 15-20 µm, as characteristically reported for *P. subniten*s (7, 8, 14).

Average temperatures during these two months were determined to be 13°C cooler than the previous 30-year average for this area, coinciding with rainfall 12 cm higher. Disease incidence in this beet field was estimated to range between 20 and 25%, although pycnial lesions were restricted mainly to the young cotyledons.

This particular field was then monitored 5 to 6 times during the remainder of the 2009 season to ascertain whether the infection could also be due to beet rust, a completely distinct disease caused by the macrocyclic but autecious pathogen *Uromyces betae* (8). Since no uredial pustules were ever observed on any sugar beet plants, beet rust was effectively ruled out as the causative factor in this field. This infested sugar beet field was additionally documented to be surrounded by stands of inland saltgrass also infected with the telial stage of a rust pathogen (Fig. 10) (9, 14).

**SURVEY OF SUGAR BEET FIELDS, 2009-2010**

Based on this unusual initial identification of the disease in Morrill County, Nebraska, in mid-May 2009, a survey of sugar beet production fields throughout the western Nebraska Panhandle was conducted between late May and mid-June to further document the incidence and number of fields infested with seedling rust caused by *P. subniten*s. After concurrent
environmental conditions were experienced in the late spring of 2010, another similar survey was conducted from more than thirty locations throughout western Nebraska (9,10).

Over this two year period, 88 locations from eight western Nebraska counties (Scotts Bluff, Morrill, Box Butte, Banner, Kimball, Sioux, Cheyenne, and Sheridan) were scouted and 47 were identified with sugar beet plants infected with pycnia and/or aecia of *P. subniten*s. Forty-one of these locations were sugar beet fields, with 36% (15/41) of the fields additionally containing infected lambsquarters (10). Infected lambsquarters were identified from several other locations throughout the area, including ditchbanks, an uncultivated field, a home garden, and a flower bed in a restaurant parking lot in Scottsbluff, Nebraska (Fig. 11).

The majority of the pathogen-infested fields (85%) during these two years were located within the North Platte Valley (Scotts Bluff and Morrill Counties) (10). Although the pathogen was readily found throughout both years, the incidence within and among sites was lower in 2010 with only 30% of the monitored locations yielding infected plants compared to 65% in 2009 (9,10).

**THE RED RUST DISEASE OF SPINACH**

Another economically important Chenopodiaceous plant that can be infected by *P. subniten*s is spinach. On spinach, the disease is called “red rust” to differentiate it from the chronic spinach disease “white rust,” which is a water mold (oomycete) in the genus *Albugo* and not a rust pathogen at all (19). The pycnial pustules of red rust are characterized by small yellow spots with red centers that appear on upper leaf surfaces of spinach (Fig. 12). Aecial clusters are scattered profusely on both leaf surfaces (Fig. 13), often arranged in rings (Fig. 13, inset) in a similar manner as that with the previously discussed sugar beet and lambsquarters species.

The first description implicating this pathogen with any type of substantial crop damage was from the Pacific Northwest in 1922 (4). H. P. Barss reported that vegetable growers in the Walla Walla Valley of Oregon and Washington sustained severe losses to their spinach crops during the spring of 1922. He also mentioned that this condition had never been observed in recent memory by anyone associated with spinach production in this region, making it a new report (4). Because no other rust disease of spinach was known at that time, it was postulated that some unknown but indigenous rust pathogen was responsible for the infection. *Puccinia subniten*s was then suspected as the cause, and after a brief survey was conducted, saltgrass was determined to be one of the three most commonly found grass species growing in the vicinity of spinach production fields in this area.

It was not until the 1940s, that this disease made another reported appearance. It was first identified on spinach from Colorado from multiple fields over two sequential seasons (1943-1944) (16,17). Since that occurrence, the disease has appeared only sporadically with severe losses experienced in 1952 and 1959 with additional reports of outbreaks in 1996 and 1999 from Colorado spinach production (19).

A survey conducted in the summer of 1959 identified the telial stage of the pathogen infecting saltgrass from 14 distinct counties, widely scattered across Colorado (12). Therefore, it was concluded that spores from the saltgrass were the likely sources...
for the spinach infections during 1943-1944 and the epidemics of the 1950s. It was additionally noted that cultivated plant hosts for the aecial stage (spinach and sugar beets) were not always present in the vicinity of the infected saltgrass to complete the life cycle, but it was concluded that wild plants in a variety of families as determined by Bethel were readily available and likely served as aecial hosts (13).

The damage to Colorado spinach production was induced both in the field and in storage while being transported to market. The first epidemics in 1943-1944 reported that infections within some fields were minor while other fields had to be destroyed due to severe leaf spotting on 50-90% of plants, making the crop unmarketable (19,20). In the 1950s the disease was shown to progress rapidly on plants during transit to market, resulting in a useless product upon arrival (18). This clearly illustrated one of the distinguishing characteristics of the disease on this plant, compared to that on sugar beets. Spinach plants undoubtedly became infected in the field similar to sugar beets, but decomposed rapidly after infections were undetected by packers prior to shipping. Even with our advanced shipping technology today, this disease is still difficult for packers to detect, creating legitimate concerns because disease and accompanying decay by invading secondary organisms can develop so rapidly during transit (16,17).

CONCLUSIONS

Sugar beet seedling rust, caused by *Puccinia subnitens*, is a disease that has rarely been observed (or at least reported) in commercial sugar beet production. To my knowledge, the two reports from Nebraska in 2010-2011 (9,10) represent the first published accounts of the natural occurrence of this disease on sugar beets in the field since the original communication in 1914 by Pool and McKay (15).

The initial report of this disease from Colorado indicated that infection appeared to be limited primarily to cotyledons (Fig. 14) with symptoms being found occasionally on the first true leaves (Fig. 15), resulting in the common name of “seedling rust” for the disease (8,15). The two-year survey conducted in Nebraska during the 2009-2010 growing seasons additionally documented the occurrence of multiple infections from many of the surveyed sites, with 20% of fields (18 of 88) from both years yielding plants exhibiting pycnial lesions on newly emerged leaves in mid to late June (10). These findings proved that the release of multiple flushes of basidiospores of the pathogen readily occurred after May from the saltgrass host, followed by new infections on sugar beets long past the cotyledon or first true leaf stage (up to the 5-6 true leaf stage) (Fig. 16).

The reverend J. M. Bates observed aecial infection by the pathogen on a wide range of weed species in Nebraska and then astutely correlated these infections with the disease of saltgrass. Nevertheless, the discovery in 2009 proved to be the first report of the disease on sugar beets in Nebraska and the first in almost 100 years from a naturally-occurring field epidemic (9,10). By correctly diagnosing the disease rapidly that first year, the needless applications of fungicide were avoided. Furthermore, the study of this disease has been valuable for its documenting of a new report of an obscure disease, while also providing a foundational baseline for recognizing future outbreaks.

Irrespective of the recent reports from Nebraska (9,10), seedling rust infection is still apparently very rare in occurrence on sugar beets. It was noted extensively in 2009, less commonly in 2010, but not at all in 2011, although it was still commonly found infecting lambsquarters in all three years. This suggests that the primary host, saltgrass, was present somewhere in the immediate vicinity of affected fields. These observations further

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**FIGURE 14**
Field-infected, young sugar beet plant exhibiting both pycnial and aecial lesions that are restricted to the cotyledons.

**FIGURE 15**
Pycnial lesion on one of the first true leaves of an infected sugar beet plant.

**FIGURE 16**
Sugar beet plant in the 5-6 leaf growth stage exhibiting a pycnial lesion of *P. subnitens* with a close-up of pycnial lesion (inset).
indicate that environmental conditions for disease were still conducive, but perhaps also suggested that lambsquarters is more susceptible to infection than are sugar beets. Sugar beet seedling rust, in general, is favored by wet and cool conditions in the spring, but optimal conditions for disease development have not been completely addressed scientifically for any host due to the rarity of its appearances, even after more than 100 years of sugar beet production in this region.

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LITERATURE CITED