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Some dynamics of spread and infection by aeciospores of *Puccinia punctiformis*, a biological control pathogen of *Cirsium arvense*

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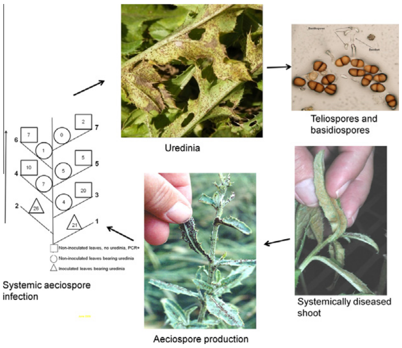
HIGHLIGHTS

- Aeciospores of *P. punctiformis* do not spread far or germinate well.
- Optimum aeciospore germination conditions occurred from late May to early June.
- Infections of *C. arvense* by aeciospores were weakly systemic.
- Conversion to teliospores took 63 days after aeciospore inoculation.
- Aeciospore infections initiate epidemics of systemic rosette infections.

GRAPHICAL ABSTRACT



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ABSTRACT

Systemic disease of *Cirsium arvense* caused by *Puccinia punctiformis* depends on teliospores, from telia that are formed from uredinia, on *C. arvense* leaves. Uredinia result from infection of the leaves by aeciospores which are one main source of dispersal of the fungus. However, factors governing aeciospore spread, germination, infection, and conversion to uredinia and telia have not been extensively investigated. In this study, effective spread of aeciospores from a source area in a field was fitted to an exponential decline model with a predicted maximum distance of spread of 30 m from the source area to observed uredinia on one leaf of one *C. arvense* shoot. However, the greatest number of shoots bearing leaves with uredinia/telia was observed within 12 m of the source area, and there were no such shoots observed beyond 17 m from the source area. Aeciospore germination under laboratory conditions was low, with a maximum of about 10%. Temperatures between 18 °C and 25 °C were most favorable for germination with maximum germination at 22 °C. Temperature and dew point data collected from the Frederick, MD airport indicated that optimum temperatures for aeciospore germination occurred in late spring from about May 18 to June 20. Dew conditions during this period were favorable for aeciospore germination. A total of 122 lower leaves, 2 per shoot, on 61 *C. arvense* shoots were individually inoculated in a dew tent in a greenhouse by painting suspensions of aeciospores onto the leaves. Of these inoculated leaves, 47 produced uredinia within an average of 21.2 ± 6.9 days after inoculation. Uredinia were also produced, in the absence of dew, on 17 non-inoculated leaves of 12 shoots. These leaves were up to 4 leaves above leaves on the same shoots that had been individually and separately inoculated. Results of PCR tests for the presence of the fungus in non-inoculated leaves that were not bearing uredinia, showed that 44 leaves above inoculated

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leaves on 27 shoots were positive for the presence of the fungus. These leaves were up to 5 leaves above inoculated leaves on the same shoot. Uredinia production and positive PCR results on leaves above inoculated leaves on the same shoot indicated that aeciospore infection was weakly systemic. In other tests in which all leaves of plants were spray-inoculated with aeciospores, uredinia were produced by 10 days after inoculation and converted to telia and sole production of teliospores in about 63 days after inoculation. Successful systemic aeciospore infections in late spring would be expected to result in uredinia production in excess of a 1:1 ratio of aeciospore infections to uredinia and ultimately telia production in late summer. In this manner, systemic aeciospore infections would promote increased density of telia that lead to systemic infections of roots in the fall.

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1. Introduction

Canada thistle (California thistle, creeping thistle, *Cirsium arvense* (L.) Scop., Asteraceae, CT), is a perennial weed of agro-ecologies in the temperate areas of the world (Guiggisberg et al., 2012; Morishita, 1999). It is native to southeastern Europe and North Africa and was introduced from there to other temperate areas. In both native and introduced ranges CT causes considerable yield loss through competition (Donald, 1994) and allelopathy (Bendall, 1975; Stachon and Zimdahl, 1980). Vegetative spread of CT through horizontal growth of the root system and emergence of adventitious shoots results in clonal patches up to 25 m or more in diameter with root depths of several meters (Donald, 1994; Hamdoun, 1970). Recommended control of CT focuses on killing the root system (Beck, 2008) and involves repeated herbicide applications and mowing over several seasons (Beck and Sebastian, 2000; Beck, 2008). However, these controls are prohibitively costly on low-value land.

Biological control offers a host-specific and low-cost management strategy for CT. The obligate rust fungus *Puccinia punctiformis* (F. Strauss) Rohl. (=*Puccinia suaveolens* (Pers.) Rostr. = *Puccinia obtegens* (Link) Tul.) was proposed as a biological control agent for CT in 1893 (Wilson, 1969). The fungus can systemically infect CT (French and Lightfield, 1990), and systemic infections result in permanent infection of the roots (Cockayne, 1915; Menzies, 1953). Systemically diseased plants and all of the shoots on infected root systems eventually die (Watson and Keogh, 1980). Gradually, entire systemically diseased CT patches die and disappear (Berner et al., 2015). In 2013, Berner et al. clarified the disease cycle of the rust and demonstrated that rust epiphytotics can be easily initiated by inoculation of rosettes in the fall with telia-bearing leaves.

Fig. 1. Undersides of leaves of Canada thistle bearing telia of *Puccinia punctiformis* from aeciospore infections in late spring and early summer.

The disease cycle begins with systemically diseased shoots of CT that emerge in the spring and bear fragrant orange-colored haploid spermagonia (Rostrup, 1874; Connick and French, 1991). After fusion of spermagonia of opposite mating types from different plants (Buller, 1950; Menzies, 1953) the systemically diseased shoots give rise to brown aecia bearing dikaryotic aeciospores, which become wind-born and cause local infections of neighboring thistle shoots and leaves in late spring and early summer (Cockayne, 1915; Olive, 1913; Rostrup, 1874; Waters, 1928). These local infections result in the development of uredinia on leaves of nearby shoots. Uredinia, and urediniospores, are morphologically indistinguishable from aecia and aeciospores (Kirk et al., 2001), but the two spore types are functionally different. Aeciospores are voluminous, extremely friable, and readily wind-blown while urediniospores are neither voluminous nor particularly friable. Rather, they are embedded in leaf tissue and gradually transition to diploid telia and teliospores in late summer (Cockayne, 1915; Buller, 1950; Menzies, 1953; Bailiss and Wilson, 1967; Kirk et al., 2001; Berner et al., 2015) (Fig. 1). Although telia and teliospores can be formed directly from aecia, this occurs under low-light conditions and extended periods of darkness (Waters, 1928) and is atypical. As CT plants senesce in the fall, leaves bearing telia abscise, fall, and are blown onto newly emerging rosettes (Berner et al., 2013). Teliospores from telia in abscised leaves germinate on the rosettes and give rise to basidiospores (Buller, 1950; French and Lightfield, 1990; Van den Ende et al., 1987). The basidiospores infect the rosette, and the rust establishes itself as mycelium in the rootstock (Bailiss and Wilson, 1967; Olive, 1913; Rostrup, 1874) where it survives perennially or until it kills the CT plant (Watson and Keogh, 1980).

Natural dispersal of *P. punctiformis* to disease-free CT patches is short distance and is effected by aeciospores, that are wind-dispersed from systemically diseased shoots, and telia that are dispersed in wind-blown leaves (Berner et al., 2013). However, the factors governing aeciospore spread, germination, infection, and conversion to uredinia and telia have not been extensively investigated. The objectives of this study were to determine: (1) distance that aeciospores spread from systemically diseased shoots to healthy plants; (2) effect of temperature on aeciospore germination; (3) extent of post-inoculation aeciospore infection within shoots; and (4) the time required from aeciospore inoculation to uredinia formation and conversion of uredinia to telia.

2. Materials and methods

2.1. Effective aeciospore spread

The maximum effective distance that aeciospores spread in the field was determined by counting shoots with at least one leaf