Root-Lesion Nematodes Affecting Dryland Cereals in the Semiarid Pacific Northwest U.S.A.

Richard W. Smiley[†]

Emeritus Professor of Plant Pathology, Oregon State University, Columbia Basin Agricultural Research Center, Pendleton, OR, U.S.A.

Abstract

Root-lesion nematodes (*Pratylenchus* spp.) are parasites that invade and deteriorate roots, thereby reducing the efficiency of water and nutrient uptake. *Pratylenchus neglectus* and *P. thornei* are the two species that are most prevalent and cause reduced yields of rainfed wheat and barley in semiarid regions of the Pacific Northwest. They are particularly damaging where wheat and barley are produced without irrigation in areas receiving less than 450 mm (18 in.) of precipitation annually. This review is focused on the biology and management of *P. neglectus* and *P. thornei* in semiarid rainfed agriculture. Characteristics of climates, soils, and crop production systems are described as a preface to constraints placed upon management options. Discussions include the economic importance, host ranges, and protocols for sampling and species identification. Discussion of

disease management options include crop rotation, genetic resistance and tolerance, planting date, trap and biofumigant crops, crop nutrition, chemical and biological nematicides, and tillage. Predictions for rainfed agriculture in a period of changing climate are presented, as are suggestions for important areas of research including crop genetics, nematode testing, and communication of results, *Pratylenchus* biology, mechanisms of resistance, the phytobiome, and closing the “yield gap” between actual and attainable yields.

Keywords: cereals and grains, crop type, cultural and biological practices, disease management, field crops, fungi, nematodes, pathogen detection, techniques

Root-lesion nematodes (RLNs; *Pratylenchus* spp.) are root parasites that reduce growth and yield of annual and perennial plants throughout the world (Castillo and Vovlas 2007). In North America, RLN damage to field crops is reported in northern Mexico (Nicol and Ortiz-Monasterio 2004; Van Gundy et al. 1974), eastern Canada, and states of the Northeast (Townshend et al. 1978; Yu 1997), Great Plains (Armstrong et al. 1993; May et al. 2016; Russell and Singleton 1984; Todd et al. 2014), and Pacific Northwest (PNW) (Hafez et al. 2010; Kandel et al. 2013; Smiley et al. 2004b; Strausbaugh et al. 2004) in the United States.

This report is focused on RLNs that invade roots of rainfed cereals (wheat [*Triticum aestivum*] and barley [*Hordeum vulgare*]) in semiarid regions of the PNW (Fig. 1) states of Oregon, Washington, and Idaho where, each year, winter wheat is produced on 1.2 million ha (2.6 million acres), spring barley on 0.9 million ha (2.0 million acres), and spring wheat on 0.3 million ha (0.7 million acres) (USDA-NASS 2017). The value of sales from these crops during 2017 was \$1.3 billion for wheat and \$260 million for barley. Impacts of RLNs on rainfed crops under semiarid conditions contrast with

more recognized RLN damage to higher-value crops produced in regions that receive greater precipitation, summer rainfall, or supplemental irrigation (Barker et al. 1998; Castillo and Vovlas 2007; Zasada et al. 2018). An appreciation of dryland (rainfed) agriculture is important for understanding the ecology and impact of RLNs in the semiarid PNW.

Dryland Agriculture

Schillinger et al. (2006) defined dryland agriculture in the western United States as production of crops without irrigation in areas having less than 600 mm (24 in.) annual precipitation. Dryland production of small-grain cereals occurs on 4.9 million ha (10.8 million acres), of which the majority (76%) is in eastern and central Washington, northern Idaho, and eastern and north-central Oregon (Fig. 1). The remainder occurs in California (4%) and intermountain regions (20%) of southeastern Idaho, western Montana, and northern Utah. Regions excluded by this definition are high-precipitation areas west of the Cascade Mountains in Oregon and Washington.

These dryland areas have a temperate Mediterranean climate, with 70 to 90% of the annual precipitation occurring from autumn through spring (October to June), coinciding with growth of winter wheat from planting to grain fill (Williams and Wuest 2021). A typical climate scenario is shown as Figure 2. Winters are cool to cold and, in some areas and years, soils may periodically freeze to depths exceeding 30 cm (12 in.). Warm summers have low relative humidity, potential evaporation that greatly exceeds rainfall from late spring until early autumn, and rapid evaporation of small rainfall events that are recorded as part of the total but only temporarily moisten the soil surface. These conditions contrast with the Great Plains, where total precipitation is often similar but distributed into

[†]Corresponding author: R. W. Smiley; richard.smiley@oregonstate.edu

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summer months. Many crops that are productive in the Great Plains do not grow well in the PNW.

Soils in dryland cropping areas of the PNW are mostly deep silt loams with low soil organic matter content (<1 to 3%) in the surface 10 cm (4 in.) (Schillinger et al. 2006). Soils are generally capable of storing sufficient winter precipitation to retain as much as 30 cm (12 in.) of plant-available water into late summer. Profitable production of dryland cereals in this region is totally dependent on stored winter precipitation and the ability of plants to extract soil water from considerable depths late in the crop life cycle.

Schillinger et al. (2006) distinguished three precipitation zones for the semiarid PNW. The low-precipitation zone occurs in Washington and Oregon and receives 150 to 300 mm (6 to 12 in.) (Fig. 1). It is the largest (36%) dryland agricultural zone in the western United States. Most crop production (90%) consists of a 2-year rotation of winter wheat (10-month growing season) and fallow (14 months). Recently, some growers have attempted diversification by planting some acreage to winter pea (*Pisum sativum*), winter canola (*Brassica napus*), or winter triticale ($\times$ *Triticosecale*) (Cann et al. 2020). However, a low-protein, soft-white winter wheat is the highest yielding crop that provides the greatest economic return and satisfies a unique marketing niche for the region. Fallow during the winter following grain harvest, and through the following summer, is essential to store a portion of winter precipitation for the next crop of winter wheat, and to reduce economic risk due to fluctuations of annual weather. Cultivated fallow allows farmers to plant and successfully establish winter wheat stands during late summer or early autumn. Farmers that utilize noncultivated fallow (no-till) must await autumn rains to plant, which occurs one or more months later than the time wheat is planted by farmers that utilize cultivated fallow (Williams and Wuest 2021).

The intermediate-precipitation zone also occurs mostly in Washington and Oregon. It is the second largest segment (22%) of dryland agriculture in the western United States and receives 300 to 450 mm (12 to 18 in.). Cropping systems are mostly a 2-year winter wheat-fallow sequence and 3-year rotations of winter wheat-spring crop-fallow, with spring crops being mostly barley, canola (*B. campestris*), or chickpea (*Cicer arietinum*). The high-precipitation zone in Washington, Idaho, and Oregon receives 450 to 600 mm (18 to 24 in.) and includes 19% of dryland agriculture in the western United States. Annual cropping commonly includes 2-year rotations of winter wheat with spring pea (*P. sativum*), lentil (*Lens culinaris*), or chickpea.

This article addresses RLNs that occur in the low- and intermediate-precipitation zones, which represent 58% of all dryland agriculture in the western United States. Crops for potential insertion into the wheat-based cropping systems in these zones have been studied for more than a century, including food legumes (pea, chickpea, and lentil), forage legumes (winter pea), oilseed (camelina

[*Camelina sativa*], canola, lupin [*Lupinus luteus*], mustard [*B. juncea* and *Sinapis alba*], sunflower [*Helianthus annuus*], and safflower [*Carthamus tinctorius*], cereals (spring wheat, oat [*Avena sativa*], and barley), and many others (Smiley 2020). All except wheat and barley have failed to gain acceptance due, in part, to a lack of profitable markets or the inability of crops to accumulate adequate heat units for maturation.

The Pathogens

The genus *Pratylenchus* includes about 70 species, at least 8 of which are parasitic to wheat and barley (Castillo and Vovlas 2007; De Waele and Elsen 2002; McDonald and Nicol 2005). *Pratylenchus crenatus*, *P. neglectus*, *P. penetrans*, and *P. thornei* are widely distributed in temperate, cereal-producing regions of the world (Castillo and Vovlas 2007; Loof 1978; Mokriani et al. 2019; Siddiqi 2000; Smiley and Nicol 2009). All four species occur in the PNW but the only widespread and economically important species in dryland fields are *P. neglectus* (Rench 1924) Filipjev and Schuurmans Stekhoven 1941, and *P. thornei* Sher & Allen 1953 (Hafez et al. 2010; Kandel et al. 2013; May et al. 2016; Smiley et al. 2004b; Strausbaugh et al. 2004).

Pratylenchus spp. are vermiform (worm-shaped) in all except the egg stage (Fig. 3). The adults are about 0.5 mm (1/64 in.) long and

Fig. 2. Monthly precipitation (millimeters), pan evaporation (millimeters), and soil temperature (°C) at a 10-cm (4-in.) depth, averaged from daily records at Moro, OR since 1911. Annual precipitation averages 282 mm (11.1 in.), with a range from 150 to 430 mm (5.9 to 16.9 in.). Planting and harvest dates are shown for spring wheat (SW) and winter wheat (WW). Recent average productivity of higher-yielding winter wheat cultivars in a wheat-fallow rotation ranged from 3.9 to 5.2 t/ha.

Fig. 1. Google Earth map of the western United States (left), with a white box designating the Inland Pacific Northwest area expanded (right) to show distributions of low, intermediate, and high dryland precipitation zones for cultivated crops in Washington, Oregon, and northern Idaho. Precipitation areas shown in this map represent 76% of all dryland agriculture and most wheat production in the western United States. Mean annual precipitations at Lind, Moro, Pendleton, Pullman, and Moscow are 243, 282, 432, and 530 mm (9.6, 11.1, 17.0, and 20.9 in.), respectively. The precipitation map was modified from Schillinger et al. (2006).

0.02 mm (1/1,000 in.) in diameter (Castillo and Vovlas 2007; Handoo and Golden 1989; Loof 1978). The diameter of a human hair (0.1 mm; 1/32 in.) is five times greater than that of an RLN.

P. neglectus and *P. thornei* reproduce by mitotic parthenogenesis (Castillo and Vovlas 2007; Loof 1978). Although males are absent or rare, low percentages of males have been reported, particularly in pure isolates maintained for use in experiments. An amphimictic species, *P. penetrans* (Cobb) Filipjev and Schuurmans Stekhoven, is often the most prevalent *Pratylenchus* sp. in irrigated, sandy soils of the PNW (Forge et al. 2000; Hafez et al. 1992) but is not common in nonirrigated silt loams (Smiley et al. 2004b). Reasons for this difference in species habitat are unknown. Perhaps dry environments favor parthenogenic species that have no need to mate to complete the reproductive cycle.

Intraspecific diversity among *Pratylenchus* populations has been reported for six species (De Waele and Elsen 2002), including *P. neglectus* on alfalfa (*Medicago sativa*), barley, and potato (*Solanum tuberosum*) (Al-Khafaji et al. 2019; Griffin 1991; Hafez et al. 1999). Although the potential impact of *P. neglectus* pathotypes on wheat is unknown, results were similar when specific wheat and barley cultivars have been screened for susceptibility to local populations of *P. neglectus* and *P. thornei* in Australia, Mexico, Turkey, and the PNW.

P. neglectus and *P. thornei* attain damaging population densities even in the driest of rainfed wheat-producing regions (Smiley et al. 2004b). They occur in clays, clay loams, silt loams, loams, and irrigated sands (Castillo and Vovlas 2007; Griffin 1996). Both species survive in an inactive, dehydrated (anhydrobiotic) state in roots or in soil during dry conditions (Glazer and Orion 1983; Talavera and Vanstone 2001; Taylor and Evans 1998). Populations decline during long periods of bare fallow between crops, with the rates of decline being greatest when soil is dried rapidly, as occurs near the surface and particularly in cultivated fallow (Thompson et al. 2017a, b). High rates of survival can occur at soil depths greater than 15 cm (6 in.), especially in fields where volunteer cereals or susceptible weed species are allowed to grow during the interval between harvest and planting (Orion et al. 1984; Smiley 2015b; Talavera and Vanstone 2001).

Life Cycle and Disease Process

The *Pratylenchus* life cycle ranges from 45 to 65 days, depending on species, presence of living roots of a susceptible plant, and a favorable soil temperature and moisture (Castillo and Vovlas 2007). Reproduction of *P. neglectus* and *P. thornei* is greatest at temperatures between 20°C (68°F) and 25°C (77°F) but may continue slowly at temperatures as low as 8°C (45°F) (Umesh and Ferris 1992). The average monthly soil temperature at Pendleton, OR (Abbe 1905) is above 8°C (45°F) at a 10-cm (4-in.) depth for

8 months (April to November), above 15°C (58°F) at all depths to 60 cm for 5 months (May to September), and above 20°C at all depths to 30 cm for 3 months (June to August). Therefore, these *Pratylenchus* spp. are well adapted for feeding and reproducing during most of the year in temperate climates of the PNW.

Pratylenchus spp. deposit eggs inside root cells and in soil. At appropriate soil temperatures, females deposit up to five eggs per day (Linsell et al. 2014b). The first-stage juvenile molts within the egg to become a second-stage juvenile (J2). A J2 can emerge from the egg about 1 week after the egg is deposited, or remain in the egg for a long period. Two additional molts within 35 to 40 days result in the adult stage. Free-living juveniles (J2 and J3) and adults are capable of feeding as ectoparasites on root hairs (Zunke 1990). They probe the root hair to identify a favorable feeding site and then use repeated thrusts of the stylet to penetrate that cell. After the stylet is embedded, the nematode injects enzymes that liquefy plant cellular cytoplasm. Following salivation, the nematode begins to ingest plant cytoplasm. After a short feeding period, the nematode moves to another root hair or another location on the same root hair. Root hairs ultimately die.

Juveniles and particularly the adult stage are also capable of penetrating and entering more robust epidermal cells in mature as well as immature root segments. In mature root segments, it is common for juveniles to follow entrance channels created by an adult. As the nematodes exhaust the supply of nutrients within a cell, they migrate endoparasitically to other root epidermal and cortical cells, or exit the root, migrate through the moisture film surrounding soil particles, and enter another root. These migratory ecto-endoparasites require sustenance from living roots to complete their life cycle. They destroy epidermal and cortical parenchyma cells to form cavities in the root cortex (Baxter and Blake 1968; Kasapoğlu Uludamar et al. 2020). The number of nematodes in root tissue increases exponentially during the growing season, and densities of several thousand nematodes per gram of dry root tissue are common. Although RLNs destroy root cells throughout the life of the plant, and they greatly reduce the number of root hairs and extent of root branching, they do not kill plants (Zunke 1990).

Colonized root segments do not usually exhibit signs of necrosis in plants younger than 3 weeks old. Cavities in the cortex begin to appear during the third week after roots were first colonized, and cavities enlarge as the nematodes feed on adjacent cells. Damaged cells “leak” cytoplasmic constituents, leading to secondary colonization by microbes and microfauna that feed on dead or decaying organic matter (Bergeson 1972). Also, RLNs defecate frequently as they feed (Baxter and Blake 1968), which would encourage secondary colonization.

Cortical degradation and reduced root branching become visible in plants older than about 6 weeks, at which time roots begin to look

Fig. 3. *Pratylenchus thornei* (left) and *P. neglectus* (center and right). Adult female and eggs in root cortical tissue (left and center; transparent nematodes were stained to distinguish them from cortical cells), and microphotograph showing the protrusible stylet, which is about 16 μ m (0.005 in.) long (right). Photos (left to right) courtesy of Dr. John Thompson (Institute of Agriculture and the Environment, University of Southern Queensland, Toowoomba, Queensland, Australia), Dr. Vivien Vanstone (Department of Agriculture and Food, South Perth, Western Australia), and Dr. Lynn Carta (United States Department of Agriculture–Agricultural Research Service, Beltsville, MD).

“thin” (Fig. 4) and may exhibit zones of deep brown to black discoloration. Much of the discoloration is due to colonization of damaged tissues by secondary colonists.

Symptoms on Wheat and Barley

Foliar symptoms on small-grain cereals are nonspecific (Doyle et al. 1987; Orion et al. 1984; Smiley et al. 2005b, c; Thompson et al. 1995; Van Gundy et al. 1974). No specific symptoms are apparent in foliage of most wheat crops affected by RLNs on the fertile silt loams of the PNW. Discovery of RLN damage occurs when a grower or advisor detects a long-term decline of grain yield that did not correspond to seasonal or annual weather patterns or the presence of other identifiable reasons. Other discoveries have been made when winter wheat has been perceived to resume foliar growth later and less vigorously than anticipated as soils become warmer during early spring. In these instances, further scrutiny can reveal the presence of RLNs in roots and soil, and plants can exhibit one or more symptoms such as impaired vigor, yellowing and premature death of lower leaves, slight stunting, reduced tillering, an increase in foliar temperature (indicating impaired leaf cooling due to restricted water uptake), delayed maturation, reduced grain yield, and reduced grain quality (Smiley et al. 2005b; Thompson and Clewett 2021a). Damage to foliage and roots is easily confused with other maladies such as nitrogen deficiency, low water availability, and root and crown diseases caused by fungi such as *Pythium*, *Rhizoctonia*, and *Fusarium* spp. (Smiley et al. 2009). Farmers, advisors, and scientists routinely fail to recognize the impact of RLNs on dryland wheat and barley.

Proving whether yield reductions are caused by RLNs generally requires a side-by-side comparison of growth in soils with

Fig. 4. Damage to wheat roots caused by root-lesion nematodes, showing a general absence of branch roots along the main root axis and a “thin” appearance of roots caused by degradation of the epidermal and cortical tissues. Photo courtesy of Dr. Vivien Vanstone, Department of Agriculture and Food, South Perth, Western Australia.

high and low densities of a RLN. The differential densities can be developed by planting “good” and “poor” hosts in close proximity for a number of years before planting a test crop uniformly over the pretreatments (Thompson et al. 2008, 2021). A more rapid method is to compare spring wheat planted into adjacent strips of untreated soil and soil treated with a nonfumigant nematicide that does not also suppress survival of soilborne plant-pathogenic fungi (Kimpinski and Johnston 1995; Thompson et al. 2012). For instance, *Pratylenchus* damage has been repeatedly demonstrated in spring crops by applying test strips of the nematicide aldicarb at the time of planting (Fig. 5) (Griffin 1996; Kimpinski et al. 1987; Smiley 2009a; Smiley et al. 2014a; Taylor et al. 1999; Thompson and Clewett 2021a; Thompson et al. 2012). Aldicarb application doubled the yield of spring wheat (Smiley et al. 2005b, c) and rangeland grasses (Griffin 1996) where stands were previously considered “normal” for that location. However, aldicarb is not registered for commercial use on cereals in the United States, and treatments applied at the time of planting do not persist long enough to inhibit invasion of RLNs into roots of winter wheat during the spring (Smiley 2009a).

Effects of RLNs on grain yield can also be evaluated on fields with high spatial variability in the native population (Taylor and Evans 1998). Densities near the surface often vary greatly over very short horizontal distances (Fig. 6). Plots are marked in such fields and are sampled to determine preplant RLN heterogeneity before the experimental area is planted uniformly. After grain harvest, regression analysis is used to examine associations between initial nematode densities and grain yield (Fig. 6).

Distribution and Economic Importance

P. neglectus or *P. thornei* have been detected in as many as 90% of fields sampled in dryland cereal-producing regions of Idaho (Hafez et al. 1992; Strausbaugh et al. 2004), Montana (Al-Khafaji et al. 2019; May et al. 2016), Oregon (Smiley et al. 2004b), and Washington (Kandel et al. 2013; Smiley et al. 2004b).

Potentially damaging high densities have been detected in as many as 60% of dryland fields in Oregon and Washington. *P. neglectus* and *P. thornei* were detected as individual species in two-thirds of surveyed fields and as a species mixture in the other third of fields (Smiley et al. 2004b). Examples of RLN densities and species mixtures for seven experiments in three Oregon counties are shown in Table 1. Both species can reduce wheat yields by 50% (Smiley and Machado 2009; Smiley et al. 2005b, c) and, within

Fig. 5. Spring wheat cultivar Alpowa in soil infested by *Pratylenchus neglectus* near Mission, OR, showing untreated control (left) and soil treated with aldicarb when seed was being planted (right). Grain yields were 3.9 and 4.9 t/ha, and postharvest nematode densities at a 0- to 30-cm depth were 2,112 and 396 nematodes/kg. Mean annual precipitation at the site is 330 mm. Wheat production in the control treatment would have been considered normal for that field.

individual fields, the dominance of one species over another may reverse in response to changes in cropping systems (Smiley 2015a; Smiley et al. 2013a, 2014a).

Pratylenchus spp. reduce yields of dryland wheat by about 5% annually in the PNW states, causing an annual reduction of 361,000 metric tons valued at US\$51 million (Smiley 2009a). *P. neglectus* and *P. thornei* were estimated to reduce yields of spring wheat in the PNW by 31 and 18%, respectively, and winter wheat by 9 and 11%, respectively. The estimated economic loss was greater for winter wheat (\$34.3 million) than spring wheat (\$16.4 million), and greater from *P. neglectus* (\$32.7 million) than *P. thornei* (\$18.0 million). May et al. (2016) estimated that *P. neglectus* in Montana reduced winter wheat yield by 13 to 15% and spring wheat yield by 4 to 7%. Armstrong et al. (1993) reported a 37% reduction in winter wheat yield at the highest density of *P. thornei* in Colorado. Todd et al. (2014) found 77% of wheat fields in Kansas to be infested by *Pratylenchus* spp., and estimated that 8% of all wheat in the central Great Plains was at risk of yield losses of 5% or greater. *P. neglectus* and *P. thornei* were also reported as economic threats to winter wheat in Oklahoma (Russell and Singleton 1984).

Economic damage from *P. neglectus* and *P. thornei* is most acute in areas with low precipitation or an absence of late-season rainfall or supplemental irrigation (Nicol and Ortiz-Monasterio 2004). In such regions, the only economically viable cropping system is usually limited to a rainfed cereal monoculture (e.g., the 2-year winter wheat-fallow rotation). It is also in these regions where disruption of soil water and nutrient uptake from deep within the soil profile becomes most critical for successful crop development and maturation (Smiley and Machado 2009; Thompson and Clewett 2021a; Thompson et al. 2021). Plants that become subjected to true drought stress late in the growing season may suffer more severe yield loss if roots of those plants were already degraded by an RLN (Nicol and Ortiz-Monasterio 2004; Whish et al. 2014). This occurs because RLNs reduce the ability of roots to extract water and nutrients from soil (Smiley and Machado 2009; Thompson and Clewett 2021a; Thompson et al. 2012; Whish et al. 2014). For instance, these nematodes reduced by 50% the amount of water extracted from soil by winter wheat (Smiley and Machado 2009), resulting in a reduction of grain yield and leaving the remaining plant-available water in soil.

Fig. 6. Natural horizontal variability of *Pratylenchus thornei* density (nematodes per kilogram of soil) in field CBARC-1 at the Columbia Basin Agricultural Research Center, near Pendleton, OR (left). The experimental area was 218 m², containing 21 plots (1.7 by 6.1 m). For each plot, 12 soil cores were taken to a 30-cm depth and collated to determine the preplant population. Densities in this example ranged from 780 to 5,630 *P. thornei* nematodes/kg of soil, with a mean of 3,503. The experimental area was planted uniformly to spring wheat cultivar Zak, and associations between nematode densities and grain yields are shown for two fields (right). (Smiley et al. 2005a).

Table 1. Preplant heterogeneity of *Pratylenchus* spp. and proportion of *Pratylenchus* among all extractable nematodes in plots of seven experiments in three Oregon counties during 2002

County ^y	Plots ^w	<i>Pratylenchus</i> spp. ^x	Nematodes (number/kg) ^y			Nematodes (%) ^{y,z}		
			Mean	Range	SD	Mean	Range	SD
Sherman	30	67% Pn, 33% Pt	1,916	400–6,280	1,420	45	18–70	15
Umatilla-1	30	90% Pn, 10% Pt	4,268	0–18,370	5,748	4	0–18	6
Umatilla-2	30	40% Pn, 56% Pt, 4% Pp	550	0–16,500	626	29	0–92	29
Umatilla-3	30	50% Pn, 50% Pt	2,637	250–10,550	2,660	21	3–72	17
Umatilla-4	30	98% Pn, 2% Pt	7,738	390–19,000	4,968	61	16–89	21
Union-1	48	90% Pn, 10% Pt	2,459	280–25,060	3,913	12	2–53	12
Union-2	36	100% Pn	913	20–4,720	1,151	2	0–9	3

^y Sherman and Umatilla County sites were rainfed. Union County sites were irrigated.

^w Number of plots. Samples were composites of 20 soil cores taken to a 30-cm depth from each 1.7-by-6.1-m plot arranged as 10 columns by 3 rows ($n = 30$), 12 columns by 3 rows ($n = 36$), or 12 columns by 4 rows ($n = 48$).

^x *Pratylenchus* spp. were *P. neglectus* (Pn), *P. thornei* (Pt), and *P. penetrans* (Pp).

^y SD = standard deviation.

^z Most other nematodes were unidentified nonplant-parasitic species except for the following plant-parasites: Sherman (1 *Meloidogyne* and 4 *Tylenchorhynchus clarus* nematodes/kg), Umatilla-1 (103 *T. clarus* nematodes/kg), Umatilla-2 (7 *Meloidogyne* and 80 *T. clarus* nematodes/kg), Umatilla-3 (1 *Meloidogyne* nematode/kg), Umatilla-4 (1 *Meloidogyne* and 34 *T. clarus* nematodes/kg), Union-1 (113 *T. clarus* and 48 *Geocenamus brevidens* nematodes/kg), and Union-2 (7 *Meloidogyne* and 21,076 *Pratylenchus* nematodes/kg).

Pratylenchus spp. survive throughout the depth of root growth (Fig. 7) and the vertical distribution varies during wet and dry years (Ophel-Keller et al. 2008; Smiley et al. 2008a; Taylor and Evans 1998; Thompson and Clewett 2021a; Thompson et al. 1999). Peak density may occur at depths from 20 to 50 cm (8 to 20 in.) in some soils (Doyle et al. 1987; Smiley et al. 2008a; Thompson and Clewett 2021a; Thompson et al. 1999, 2021), which has a profound impact on detection, quantification, and management of these species. Although nonhost crops can reduce densities at great depth, it is virtually impossible to use tillage or nematicide treatments to significantly reduce *Pratylenchus* densities deep in the soil profile. However, significant associations observed between grain yields and RLN densities measured from shallow samplings of some experiments (Fig. 6) suggest that protection of seedling growth conveys a significantly positive effect on crop performance. Thompson and Clewett (2021a) concluded that genetic, environmental, and management factors that reduce the impact of *Pratylenchus* spp. on seedling plants have the greatest influence on wheat yield components and grain yield.

Taylor and Evans (1998) detected 64 to 94% of the total free-living *Pratylenchus* population by collecting soil samples to a depth of 20 cm (8 in.). Higher proportions were recovered from the top 10 cm (4 in.) of sands and sandy loams than from clay soils. Thompson et al. (1999) detected less than 20% of the population when sampling was restricted to the top 15 cm (6 in.). Smiley et al. (2008a) detected more than 50% of the *Pratylenchus* population at most sites by sampling to a 30-cm (12-in.) depth, and more than 75% of the population by sampling to 45 cm (18 in.). It was concluded that, for deep silt loams with unknown population characteristics in the PNW, initial samples should be collected to a 45-cm (18-in.) depth.

Sampling to a 45-cm depth was used for only one survey in this region (Hafez et al. 1992). Sampling was to a maximum of 10 cm in depth for a survey of dryland fields in Oregon and Washington (Smiley et al. 2004b). Another survey of dryland fields in Washington collected inverted cone-shaped samples to a maximum depth of 25 cm, meaning that most soil extracted to count RLNs would have been from the surface 8 cm (Kandel et al. 2018). Another survey in Idaho used samples also collected by shovel to an undescribed depth (Strausbaugh et al. 2004). It is now clear that densities and occurrences of RLNs for all recent studies of dryland agriculture in the PNW may have misrepresented reported associations between RLNs and tillage, crop rotations, and climatic factors.

Nematode Density and Grain Yield

Relationships between the number of RLNs and wheat or barley yield are difficult or impossible to generalize over large regions because crop responses are influenced by interactions with climate,

Fig. 7. Illustrations of *Pratylenchus* spp. densities at incremental soil depths following harvests of winter wheat (VW) near Pendleton (*P. thornei*) and Moro, OR (*P. neglectus*), spring wheat (SW) or spring barley (SB) near Moro, and spring mustard (SM) near Heppner (*P. neglectus*). Mean annual precipitation at Pendleton, Moro, and Heppner is 432, 282, and 312 mm, respectively. (Smiley et al. 2008a).

edaphic factors, host tolerance, and occurrences of soilborne plant-pathogenic fungi (Fanning et al. 2020). However, it is clear that relatively low population densities of RLN can create economic losses in low-rainfall environments (Fig. 6). Economic damage to wheat can be expected in most nonirrigated soils when the preplant population exceeds two nematodes per gram of soil (Armstrong et al. 1993; Thompson et al. 2008, 2020, 2021). In the PNW, densities as low as one nematode per gram of soil reduced grain yield of intolerant cultivars of spring wheat by up to 50% and higher densities reduced wheat yield as much as 70% (Smiley et al. 2005b, c). Owen et al. (2014) also indicated that economic damage occurred with RLN densities greater than one nematode per gram in Australia. Samplings of dryland fields in the PNW and Montana commonly detect *Pratylenchus* densities greater than one or two nematodes per gram of soil (Hafez et al. 1992; Kandel et al. 2013; May et al. 2016; Smiley et al. 2004b; Strausbaugh et al. 2004).

Much higher preplant densities of RLNs are required to cause economic loss in cereal crops that are provided adequate supplies of water and nutrients during late phases of the growing season. Nicol and Ortiz-Monasterio (2004) found that *P. thornei* did not influence wheat yield in routinely irrigated fields but caused up to 29% yield reduction when the crop was subjected to water stress by limiting the amount of irrigation water supplied.

Interactions with Other Pathogens and Pests

Interactions of RLNs with fungal pathogens and other plant-parasitic nematodes on most crop species were reviewed by Castillo and Vovlas (2007). On wheat, Kimpinski et al. (1976) reported that *Gaeumannomyces tritici* (= *G. graminis* var. *tritici*; take-all) reduced the magnitude of feeding sites and reproduction of *P. neglectus*. However, most reports of interactions between fungal pathogens and *Pratylenchus* spp. indicate a positive or additive effect of the two agents on reduction of plant growth or grain yield. Greater reduction of yield occurred when *P. neglectus* and *Rhizoctonia solani* (Rhizoctonia root rot, or bare patch) were both present, compared with either pathogen alone (Benedict and Mountain 1956). Compared with effects of individual pathogens, yield reduction was greater when soil was coinoculated with *P. thornei* and *Fusarium culmorum* (*Fusarium* crown rot) (Fig. 8) (Hajihassani et al. 2013) or with *P. neglectus* plus *Pythium irregulare* (*Pythium* root rot and seedling damping-off), *F. oxysporum*, or a combination of *G. tritici* and *F. equiseti* (Taheri et al. 1994). In fields naturally infested by two or more pathogens, additive responses occurred from invasions by *Pratylenchus thornei* and *F. pseudograminearum* (*Fusarium* crown rot) (Simpfendorfer et al. 2012; Thompson and Clewett 2021b), by *P. neglectus* and *F. pseudograminearum* (Smiley et al. 2004a), by

Fig. 8. Percentage reduction in yield of winter wheat inoculated with *Pratylenchus thornei* (red dotted line) at four levels of initial inoculum density (0 to 4,000 nematodes/kg of soil) or coinoculated with a single rate of *Fusarium culmorum* (black solid line). Pathogen-free soil is the zero rate of *Pratylenchus* alone. The *Fusarium*-alone control is shown as the zero rate of *Pratylenchus* inoculation. Grain yield was reduced 64% when the fungus and the nematode were both present at densities commonly encountered in wheat fields. Adapted from Hajihassani et al. (2013).

mixed *Pratylenchus* spp. and a mixture of *F. culmorum* and *F. pseudograminearum* (Smiley et al. 2016), by mixed *Pratylenchus* spp. and *R. solani* AG-8 (Smiley et al. 2016), and by *P. neglectus* and *Heterodera avenae* (cereal cyst nematode) (Lasserre et al. 1994). All of these nematodes and fungi are common in PNW dryland cropping systems (Paulitz et al. 2002; Smiley 1996; Smiley et al. 1996, 2013a, b, 2016).

No association was detected between *Pratylenchus* spp. and non-plant parasitic nematodes in dryland fields of Oregon and Washington (Smiley et al. 2004b). This was presumed due to RLNs feeding only on living root tissue and nonplant-parasitic species feeding on microflora and organic detritus in soil (Neher 2010).

Gough et al. (2020) reported both positive and negative interactions between *Pratylenchus* spp. and arbuscular mycorrhizal fungi on different crops. These fungi occupy the same root epidermal and cortical tissues, and rhizosphere soil, that are occupied by all life stages of *Pratylenchus* spp. Inoculation of crops with arbuscular mycorrhizal fungi results in relationships that vary depending on mycorrhizal species, crop species, and crop cultivar (Gough et al. 2020). Mycorrhizae in the order Glomerales generally reduce the *Pratylenchus* density, whereas species in the order Diversisporales tend to increase the *Pratylenchus* density. Wheat and other C₃ grasses with fibrous roots respond less to colonization by mycorrhizal fungi than C₄ grasses and plants with tap roots. Frew et al. (2018) reported that coinoculation of mycorrhizal fungi and *P. neglectus* on winter wheat increased the uptake of phosphorus, potassium, and zinc but also resulted in a 24% reduction of plant biomass and root weight, because the *P. neglectus* population was increased by 47 to 117%, depending on wheat cultivar. They reported that the mycorrhizal infection disarmed the benzoxazinoid metabolic pathway that contributes to *Pratylenchus* resistance in wheat roots. Sikder et al. (2021) also reported that benzoxazinoid has a role in resistance to *P. neglectus*, as determined by higher nematode reproductive rates when synthesis of that secondary metabolite was eliminated in near-isogenic knock-out mutants of maize (*Zea mays*).

Host Range

P. neglectus and *P. thornei* are capable of multiplying in a wide range of monocot and dicot hosts (Castillo and Vovlas 2007; Loof 1978; Thompson et al. 2008; Vanstone and Russ 2001a, b; Vanstone et al. 2008). Although wheat is the primary dryland crop in the semi-arid PNW, other crops are also produced and farmers would like to expand the diversity of crops. Therefore, it is important to understand hosting abilities of potential crops and cultivars to develop an effective RLN management strategy. The following discussion focuses on research in the PNW (Smiley et al. 2014b, c), which involved different cultivars but was otherwise congruous with research reported

Fig. 9. Reproductive rates (R_f) of *Pratylenchus neglectus* on selected Pacific Northwest cultivars of winter wheat, plus an unplanted control, a resistant Australian breeding line (GS50A), and resistant landrace wheat lines from Azerbaijan (AUS28451R) and Iran (Persia 20). R_f is the ratio of final population (P_f) to initial population (P_i) after a 16-week incubation period, and resistance is defined as $R_f < 5\%$ of the maximum rate in each test. (Smiley et al. 2008d).

from Australia (Hollaway et al. 2000; Taylor et al. 2000; Thompson et al. 2008; Vanstone and Russ 2001a, b; Vanstone et al. 2008).

Small-grain cereals. All tested wheat cultivars in the PNW allow moderate to high rates of reproduction for *P. neglectus* and *P. thornei* (Figs. 9 and 10) (Sheedy et al. 2007; Smiley et al. 2008b, c, d). Sources of resistance have been identified in landrace wheat lines (Sheedy et al. 2012; Smiley et al. 2014a; Thompson et al. 2009; Thompson et al. 2016), and one landrace has been incorporated into wheat improvement programs in the PNW (Figs. 11 and 12) (Thompson et al. 2015; Thompson et al. 2017a).

Reproduction of *Pratylenchus* spp. occurs on most wheat cultivars but those cultivars exhibit variable tolerance and yield stability in RLN-infested fields (Smiley 2009a; Smiley et al. 2005b, c). Application of aldicarb doubled the grain yield of intolerant spring wheat cultivars (Figs. 13 and 14) but provided little or no improvement in productivity of tolerant wheat and barley cultivars (Smiley 2009a). Cultivars with the highest tolerance to *P. neglectus* often differ from those with the highest tolerance to *P. thornei*. Similar observations have been reported from Australia (Thompson et al. 2021).

Fig. 10. Reproductive rates (R_f) of *Pratylenchus neglectus* on selected Pacific Northwest cultivars of spring wheat and spring barley, plus an unplanted control and resistant landrace wheat lines from Azerbaijan (AUS28451R) and Iran (Persia 20). R_f is the ratio of final population (P_f) to initial population (P_i) after a 16-week incubation period, and resistance is defined as $R_f < 5\%$ of the maximum rate in each test. (Sheedy et al. 2007).

Fig. 11. Roots of three spring wheat cultivars grown in cones of soil infested with *Pratylenchus neglectus*: Louise (left), AUS 28451 (center), and Alpowa (right). Roots of Louise and Alpowa are blackened by nematode-induced damage. Roots of AUS 28451 remained white because *P. neglectus* caused very little cellular damage. Louise and AUS 28451 were crossing parents of the LouAu mapping population for use in research and wheat breeding (Thompson et al. 2015). Photo courtesy of Dr. Alison Thompson, United States Department of Agriculture-Agricultural Research Service, Maricopa, AZ.

Reproduction of *P. neglectus* and *P. thornei* is much lower on most cultivars of barley than on most cultivars of wheat (Doyle et al. 1987; Sheedy et al. 2007; Smiley et al. 2008b, c, d). It follows that *Pratylenchus* populations in soil are typically lower following barley compared with wheat (Smiley 2009a; Smiley et al. 2004b, 2008a;

Fig. 12. Performance of three spring wheat cultivars averaged over 2 years in two fields infested with mixtures of *Pratylenchus neglectus* and *P. thornei*. Tests were near Mission and Pendleton, OR. Nematodes were counted after crops were harvested. Louise is susceptible and moderately intolerant, Alpowa is susceptible and intolerant, and AUS28451 is highly resistant and intolerant. (Smiley et al. 2014a).

Thompson et al. 2012). Also, reproduction of *P. thornei* and *P. neglectus* are both less on oat cultivar Monida than on susceptible wheat cultivars (Smiley et al. 2014b).

Food legumes. Reproduction of *P. thornei* is much greater than *P. neglectus* on many cultivars of pea, lentil, and chickpea (Fig. 15) (Smiley et al. 2014b). At one extreme, the multiplication rates (reproductive rates [Rf]) (Fig. 9) of *P. thornei* and *P. neglectus* on green field pea cultivar Journey were 48 and 3, respectively. In contrast, the Rf values for *P. thornei* and *P. neglectus* on chickpea cultivar Sierra were 2 and 9, respectively.

Oilseed. Reproduction of *P. neglectus* is much greater than *P. thornei* on many PNW cultivars of canola, mustard, and camelina (Fig. 15) (Smiley et al. 2014b). The Rf values for these crops ranged from 6 to 32 for *P. neglectus* and from 0.8 to 1.4 for *P. thornei*. High densities of *P. neglectus* have been reported for fields in which spring mustard was harvested as a seed crop (Smiley et al. 2008a). For both nematode species, Rf values were <1 on tested cultivars of flax (*Linum usitatissimum*), safflower, and sunflower.

Other crops. Reproduction of *P. neglectus* and *P. thornei* were nil to very low on gamagrass cultivar Pete (*Tripsacum dactyloides*) and switchgrass cultivar Blackwell (*Panicum virgatum*), both of which are of potential interest for production of biomass or biofuel crops (Fig. 15) (Smiley et al. 2014b). Reproduction of *Pratylenchus neglectus* was greater than for *P. thornei* on sudangrass cultivar Piper

Fig. 13. Grain yields averaged over 2 years for spring wheat cultivars in a field infested with *Pratylenchus neglectus* near Heppner, OR (dashed line), compared with adjacent plots planted into soil treated with aldicarb (solid line). Cultivars are arranged from highest to lowest yields in untreated soil. (Smiley 2009a).

Fig. 14. Grain yields averaged over 2 years for spring wheat cultivars in a field infested with *Pratylenchus thornei* near Pendleton, OR (dashed line), compared with adjacent plots planted into soil treated with aldicarb (solid line). Cultivars are arranged from highest to lowest yields in untreated soil. (Smiley 2009a).

(*Sorghum bicolor*) and a sorghum/sudangrass hybrid cultivar Greentreat Plus (*Sorghum* × *drummondii*).

Range grasses and forage legumes. Rangeland plants are planted and maintained as conservation plantings on large tracts of highly erodible soils in semiarid regions. These plantings are contractually regulated for 10-year renewable periods by the Conservation Reserve Program (CRP) of the United States Department of Agriculture (USDA). If wheat prices are high when CRP contracts expire, fields may be transitioned back to production of winter wheat. Damaging densities of *Pratylenchus* spp. and fungal root pathogens occur after conservation plantings are converted to wheat production, and some first crops of wheat do not perform as well as expected (Smiley et al. 2008a). When diagnosing the cause of poor performance in crops following CRP, it is important to consider the possibility that RLNs may have contributed to that outcome. If nematode populations are high, barley or another poor host should be considered as a first or second crop in the transition from CRP.

Many common rangeland grasses and forage legumes are good hosts for *Pratylenchus* spp. (Fig. 16). Good hosts for *P. neglectus* but not *P. thornei* included a tested cultivar of western wheatgrass (*Pascopyrum smithii*), tall wheatgrass (*Elytrigia elongata*), big bluegrass (*Poa secunda*), and two hairy vetches (*Vicia villosa*). Good hosts of *Pratylenchus thornei* but not of *P. neglectus* included a hard fescue (*Festuca brevipila*) and sheep fescue (*F. ovina*). Both species reproduced well on tested cultivars of smooth brome (*Bromus inermis*) and many wheatgrasses (species of *Agropyron*, *Elymus*, *Elytrigia*, and *Pseudoroegneria*) (Smiley et al. 2014c). Two rangeland cultivars of alfalfa (*Medicago sativa* subsp. *falcata* and *sativa*) were poor hosts for both nematode species.

Weeds. Weeds such as pigweed (*Amaranthus retroflexus*), palmer amaranth (*A. palmeri*), kochia (*Bassia scoparia*), tumble mustard (*Sisymbrium altissimum*), lambsquarters (*Chenopodium album*), Russian thistle (*Salsola tragus*), crabgrass (*Digitaria sanguinalis*), wild oat (*Avena fatua*), and green foxtail (*Setaria viridis*) support efficient

reproduction of *P. neglectus* but not *P. thornei* (Fig. 17) (Smiley et al. 2014c). In contrast, downy brome (*Bromus tectorum*) and rattail fescue (*Vulpia myuros*) support reproduction of *P. thornei* but not *P. neglectus*.

Jointed goatgrass (*Aegilops cylindrica*) supports high levels of reproduction by both *Pratylenchus* spp. This is particularly important in view of expanding use of herbicide-resistant winter wheat cultivars to manage weeds such as jointed goatgrass and downy brome. These crops are sprayed in the spring with an appropriate herbicide to kill or retard the winter annual grass weeds. The ability of *Pratylenchus* spp. to migrate from roots of dying plants to roots of susceptible hosts creates a scenario akin to that of the “green bridge” concept, which describes an enhanced transfer of fungal pathogens into roots of herbicide-resistant wheat after infested volunteer wheat and weed hosts are killed by herbicide application (Smiley et al. 1992, 2009).

Sampling and Extraction of Nematodes

Horizontal and vertical distributions of RLNs are affected by soil properties, moisture, temperature, host root system structure, cropping history, and other factors. Different sampling intensities, timings, patterns, and collection devices are used to meet the needs of surveys, diagnosis of crop anomalies, and research (Ingham 1994; Nickle 1991). Shallow samplings using a cylindrical soil probe or shovel may suffice for general surveys, particularly if the survey is conducted mostly to detect the sedentary endoparasitic root knot and cyst nematodes, each of which are found at shallow depths. For surveys to detect RLNs, the soil probe should be inserted to a depth of 45 cm to enumerate an acceptably high proportion of these species in dryland fields (Doyle et al. 1987; Smiley et al. 2008a; Taylor and Evans 1998; Thompson et al. 2021). In all, 10 to 20 subsamples are collected across a sampling unit (entire field, topographic feature, or experimental area) and composited in a bag or bucket. The soil is mixed and about 500 cm³ (1.1 pound, or 1 pint) is retained for extraction of nematodes.

Fig. 15. Reproductive rates (R_f) of *Pratylenchus neglectus* and *P. thornei* on selected Pacific Northwest cultivars of assorted crops. R_f is the ratio of final population (P_f) to initial population (P_i) after a 16-week incubation period, and resistance is defined as $R_f < 5\%$ of the maximum rate in each test. (Smiley et al. 2014b).

Extraction of living RLNs requires that motile juvenile and adult stages be alive when they reach the diagnostic laboratory. Samples must be collected and handled carefully because RLNs are easily killed when samples become overheated in direct sunlight or inside a

Fig. 16. Reproductive rates (R_f) of *Pratylenchus neglectus* and *P. thornei* on selected Pacific Northwest rangeland grasses (blue) and forage legumes (red). R_f is the ratio of final population (P_f) to initial population (P_i) after a 16-week incubation period, and resistance is defined as $R_f < 5\%$ of the maximum rate in each test. (Smiley et al. 2014c).

Fig. 17. Reproductive rates (R_f) of *Pratylenchus neglectus* and *P. thornei* on selected Pacific Northwest weeds. R_f is the ratio of final population (P_f) to initial population (P_i) after a 16-week incubation period, and resistance is defined as $R_f < 5\%$ of the maximum rate in each test. (Smiley et al. 2014c).

closed automobile. RLN counts can also be underrepresented when dry soils are physically fractured during sampling (Hollaway et al. 2003; Taylor and Evans 1998). This occurs because the nematodes survive in dry soils in a very brittle state of anhydrobiosis (Glazer and Orion 1983). They are easily broken and killed when dry soils are fractured. Therefore, sampling for accurate counts of living RLNs should be conducted when the soil is moist. An exception is for samples destined to be processed by a DNA-extraction method. The soil moisture content at the time of sampling does not affect DNA-based estimates of RLN numbers (Hollaway et al. 2003). Extraction of DNA includes counts of all life forms, including eggs.

Because RLNs are migratory ecto-endoparasites, counting the individuals inside roots is as important as counting those in soil. Root segments should be retained in soil samples. For diagnostic and research purposes, it is often necessary to count RLNs inside roots separately from those in soil, and to report the sum of those populations.

RLNs reach peak densities in roots of dryland field crops shortly before the crop matures. They decline during winter and periods of fallow or growth of a nonhost crop. Samplings to detect potentially high populations are best conducted after soil under wheat or barley stubble is remoistened during the autumn, or in early spring.

Nematode extraction procedures were summarized by Ingham (1994), Nickle (1991), and Southey (1986). Most common is the Baermann funnel method, which enables RLN juveniles and adults to migrate through wet soil or out of roots over periods of 2 to 7 days, during which these life stages settle to the bottom of a shallow water layer. The nematode suspension is collected and concentrated to count and identify the extracted nematodes. The Whitehead tray method is a modification of the Baermann funnel method and is widely used for applied research because it allows for larger volumes of soil to be extracted over short (2- to 3-day) time periods.

Ingham (1994), Nickle (1991), and Southey (1986) also provided details of methods to count nematodes. The extracted nematodes are concentrated into small volumes of water, from which an aliquot is viewed under a stereoscopic microscope. With practice, it is possible to distinguish *Pratylenchus* spp. from other nematode genera. It is much more difficult to use morphological characteristics to reliably distinguish among *Pratylenchus* spp. Molecular procedures are now available to differentiate (Fig. 18) and quantify (Fig. 19) *P. neglectus* and *P. thornei* in DNA extracted from either a nematode suspension or directly from the soil. These DNA-based procedures can eliminate the manual extraction process and provide counts equivalent to physical extractions (Fig. 19). DNA extractions from soil are now used in most research laboratories and in some commercial nematology laboratories (Ophel-Keller et al. 2008; Smiley 2015b).

RLNs can also be counted directly in roots. The washed roots are stained to differentiate the hyaline nematodes from root tissues (Fig. 3). The stained nematodes are then counted by direct observation using a stereoscopic microscope. This procedure does not include RLNs that were at the root surface or in soil when the roots were washed.

Fig. 18. Identification of *Pratylenchus thornei* and *P. neglectus* in naturally infested soil samples. Nematode DNA was extracted from soil and amplified with the *P. thornei*-specific primer set PTHO/D3B (top) and with the *P. neglectus*-specific primer set PNEG-F1/D3B5 (bottom). Lane M = the 100-bp DNA molecular weight ladder, lanes S4 to S30 = soil samples, lane Pc = the positive control from pure nematode cultures, and lane Nc = the negative control lacking a DNA template. (Yan et al. 2008).

Species Identification

Identification of *P. neglectus* and *P. thornei* to the species level is an essential prerequisite for most control strategies because of species-specific differences in host range and cultivar tolerance. However, identification based on morphological characteristics can be very difficult and prone to error because there are few differences of precise taxonomic value. *Pratylenchus* spp. are also notorious for having intraspecific variation as well as overlapping ranges and shapes of morphological features (Filho and Huang 1989; Handoo and Golden 1989; Loof 1978).

The most accurate identifications of RLNs involve a complementation of morphological and biochemical or molecular methods. DNA-based methods include PCR, quantitative real-time PCR, PCR-restriction fragment length polymorphism, and sequence-characterized amplified region PCR (Al-Banna et al. 1997; Carneiro et al. 2017; Carrasco-Ballesteros et al. 2007; Mokri et al. 2014; Nega 2014; Ophel-Keller et al. 2008; Orui 1996; Waeyenberge et al. 2000; Yan et al. 2008, 2012, 2013; Yu et al. 2012). Additional methods of potential use in the future include loop-mediated isothermal amplification, high-throughput droplet digital PCR, and DNA metabarcoding (Ahuja and Somvanshi 2021; Jones et al. 2016; Kawanobe et al. 2021; Notomi et al. 2000).

Disease Management

Successive or frequent plantings of susceptible wheat cultivars clearly elevate populations of *P. neglectus* and *P. thornei* and increase the level of risk to subsequent intolerant crops (Table 2) (Thompson et al. 2008; Vanstone et al. 2008). An RLN-management strategy should be considered where high numbers of RLNs are detected at any depth. However, practices to achieve that goal are

very limited. The goal is to suppress the density of nematodes to a level below that which causes economic loss. The threshold density at which RLNs begin to cause significant economic loss is variable (Thompson and Clewett 2021b) but has been suggested to be one nematode per gram of soil when samples are collected and mixed from the entire upper 90 cm (36 in.) of the soil profile (Owen et al. 2014). Another suggested threshold is two nematodes per gram of soil collected from any depth in the profile (Thompson et al. 2008).

Approximately 3 years of bare fallow or resistant rotational crops were needed to reduce high *Pratylenchus* densities to levels below a threshold for economic damage in Australia (Owen et al. 2014; Whish et al. 2017). It is also not practical to restrict spread to noninfested fields because RLNs are already widely distributed in dryland fields.

It is also very challenging to construct effective RLN management programs in regions where the economics of dryland agriculture heavily favor wheat-based monocultures and simple rotations. Production of just one crop of a susceptible wheat cultivar can reestablish RLN densities above the threshold for economic damage to a subsequent crop of an intolerant cultivar (Thompson et al. 2021). Therefore, management of RLNs will be most effective when it becomes possible to combine management options that include wheat cultivars that are both resistant and tolerant (Castillo and Vovlas 2007; McDonald and Nicol 2005; Smiley and Nicol 2009; Thompson et al. 2008, 2021; Vanstone et al. 2008). Components of potential management options to move toward that goal in the PNW are as follows.

Crop rotation. Crop rotations to manage RLNs are reliant upon accurate identification of the *Pratylenchus* spp. to be addressed, and whether mixtures of species are present. Profitable markets are also required but are lacking in the PNW for most crops other than wheat or barley. Additionally, the hosting ability of crops other than wheat or barley often depends on the nematode species and the plant cultivar. For instance, many cultivars of mustard, canola, lentil, and chickpea increase populations of either *P. neglectus* or *P. thornei* (Bernard and Montgomery-Dee 1993; Castillo et al. 1998; Fatemy et al. 2006; Potter et al. 1999; Smiley et al. 2014b). Crops that restrict multiplication of *P. neglectus* or *P. thornei* include some cultivars of barley, safflower, triticale, flax, and field pea (Esmenjaud et al. 1990; Farsi et al. 1995; Heide 1975; Hollaway et al. 2000; Lasserre et al. 1994; Riley and Kelley 2002; Smiley et al. 2004b, 2014b; Taylor et al. 2000; Thompson et al. 1995; Van Gundy et al. 1974). Therefore, routine hosting studies of all potential crops are imperative to characterize locally adapted cultivars.

Feed-type spring barley is profitable in several regions of the low- and intermediate-rainfall zones of the PNW. Local cultivars allow far less reproduction of *P. neglectus* and *P. thornei* than occurs on most cultivars of wheat (Sheedy et al. 2007; Smiley et al. 2008b, c, d) and, when inserted into wheat-based cropping systems, barley almost always reduces the *Pratylenchus* density in these soils (Table 2). Farmers in the PNW dryland region often state that yields of wheat crops are better following a crop of barley. However, 2-year rotations of winter wheat and spring barley are seldom practical

Fig. 19. Correlation between the numbers of *Pratylenchus thornei* (Pt) determined by DNA extraction and real-time PCR assay, compared with extractions of living nematodes using the Whitehead tray and counting them by using a stereoscopic microscope. (Yan et al. 2012).

Table 2. Density of *Pratylenchus* spp. for eight replicated cropping systems at Moro, OR^z

Annual crop or rotation	<i>Pratylenchus</i> spp./kg of soil	Immediately preceding crop	<i>Pratylenchus</i> spp./kg of soil
Annual spring wheat	3,017 a	Spring wheat	2,873 a
Annual winter wheat	2,305 ab	Spring mustard	2,791 ab
Winter wheat-cultivated fallow	1,653 ab	Winter pea	2,269 ab
Winter wheat-winter pea	1,486 b	Winter wheat	1,965 b
Winter wheat-chemical fallow	1,291 b	Spring camelina	659 c
Flexible cropping decisions	1,242 b	Spring barley	537 c
Winter wheat-spring barley-chemical fallow	676 c	Spring pea	376 c
Annual spring barley	352 c	—	—

^z Data for “Annual crop or rotation” were averaged by treatment over a 9-year interval (2004 to 2012) using samples collected to a 30-cm depth during the spring. Data for “Immediately preceding crop” were for samples taken after that crop was harvested, averaged over the same time period. All sequences were performed without cultivation (no-till), except the winter wheat-cultivated fallow rotation, which represented the traditional practice for the region. Cropping decisions were made annually for the “Flexible cropping decisions” treatment (Smiley et al. 2013a). Values did not differ significantly ($P < 0.05$) when followed by the same letter within each column.

because a water-conserving fallow is usually required for optimal production of winter wheat in the low-precipitation zone. Also, spring barley can become a volunteer contaminant of the following wheat crop, resulting in mixtures of wheat and barley grains that must be screened at additional expense to achieve a profitable market grade for the wheat. Alternatively, to prevent mixed-grain classes at harvest, the use of a herbicide-resistant winter wheat cultivar could be sprayed to kill volunteer barley and winter-annual grass weeds (Lyon et al. 2020).

Fortunately, barley can be profitably inserted into a 3-year rotation of a susceptible winter wheat, resistant spring barley, and fallow. Compared with a 2-year winter wheat-fallow rotation, numbers of *Pratylenchus* are much lower in the 3-year wheat-barley-fallow rotation (Smiley et al. 2013a). Similar results were reported from Australia (Thompson et al. 2012). If necessary, sources of improved resistance to RLNs in barley have also been identified internationally (Keil et al. 2009).

Genetic resistance and tolerance in wheat. Cultivars that are both resistant and tolerant to *Pratylenchus* spp. will become the most effective component of RLN management programs in the semiarid PNW (Cook and Evans 1987; Thompson et al. 1999; Trudgill 1991). Resistance and tolerance are genetically independent and are each controlled by multiple genes. Within large collections of cultivars, it is possible to identify gradients of all combinations of resistance and tolerance traits. A cultivar can be resistant and intolerant, resistant and tolerant, susceptible and intolerant, or susceptible and tolerant. Identification of these traits requires different research approaches.

Resistance. Resistance is a trait that measures the ability of a plant to restrict multiplication of an RLN (Thompson et al. 1999; Trudgill 1991). Resistant plants reduce the density of nematodes remaining in soil and the level of risk to a following intolerant crop. Resistance is generally studied in greenhouse pot trials to control uniformity of initial inoculum density and the environment. Most wheat cultivars in the PNW are susceptible to both *P. neglectus* and *P. thornei* (Figs. 9 and 10) (Sheedy et al. 2007; Smiley et al. 2008b, c, d).

Sources of significant resistance to *P. neglectus* or *P. thornei* have been identified in commercial wheat cultivars, Middle East landrace lines, and wheat relatives such as *Aegilops* spp. (McDonald and Nicol 2005; Smiley and Nicol 2009; Thompson and Haak 1997; Thompson et al. 1999, 2008; Yu et al. 2012; Zwart et al. 2004, 2005). Lines of special interest are those that exhibit resistance to both *P. neglectus* and *P. thornei* (Sheedy et al. 2007; Smiley et al. 2008b, c, d; Thompson et al. 2016; Zwart et al. 2005). Introgression of dual-resistance sources into PNW-adapted commercial cultivars (Thompson et al. 2015, 2017) has promise for eliminating the need for farmers to identify *Pratylenchus* to the species level before selecting a resistant cultivar.

Phenotypic identification of resistance and molecular methods have been used to investigate the genetic control and location of resistance genes, and the identification of markers for resistance. Quantitative trait loci (QTLs) for resistance of wheat to either *P. thornei*, *P. neglectus* or both species have been identified on all three genomes (A, B, and D) of wheat. Specific QTLs occur on all seven chromosomes of the A genome, five of seven chromosomes of the B genome (1B, 2B, 3B, 5B, and 6B), and six of seven chromosomes of the D genome (1D, 2D, 4D, 5D, 6D, and 7D) (Dababat et al. 2016; Linsell et al. 2014a; Kumar et al. 2021; Schmidt et al. 2005; Sheedy et al. 2012; Thompson et al. 2017; Toktay et al. 2006; Yu et al. 2012; Zwart et al. 2005, 2006). Likewise, resistance of barley to *P. neglectus* has been mapped to QTLs on chromosomes 1H, 3H, 4H, 5H, 6H, and 7H (Galal et al. 2014). Research on resistance to *P. neglectus* and *P. thornei* has included development of simple sequence repeat markers to track resistance QTLs in breeding programs. Associations between resistance reactions and markers such as *Rln1* (Williams et al. 2002) have been effectively applied in marker-assisted selections to improve *Pratylenchus* resistance in Australia and in the international wheat breeding program at the International Maize and Wheat Improvement Center (CIMMYT).

Unfortunately, *Pratylenchus* spp. invade and injure roots of resistant as well as susceptible plants (Kasapoğlu Uludamar et al. 2020; Linsell et al. 2014b). When a resistant wheat cultivar is sensitive

(intolerant) to initial invasion by the nematode, the invasion of the nematode can result in reduced growth and grain yield, even though reproduction of the nematode was prevented or greatly suppressed. Progress is being made toward developing cultivars with resistance plus tolerance.

Tolerance. Tolerance measures the yield capacity of the current crop, even when roots are invaded by RLNs (Cook and Evans 1987; Thompson et al. 1999, 2021; Trudgill 1991). Tolerance has no bearing on the potential for damage to the following crop because tolerant plants can be either resistant or susceptible. Tolerance is usually estimated by comparing grain yields in adjacent treatments where pre-plant nematode densities were controlled to be either high or low. Cultivars that are tolerant of *P. neglectus* are not necessarily tolerant of *P. thornei* (Figs. 13 and 14) Smiley 2009a; Thompson et al. 2021).

For comparing grain yields under high and low RLN pressure, treatments within a field are often prepared by planting strips or blocks with susceptible or resistant crops for at least several years (Nicol et al. 1999; Thompson 1992; Thompson et al. 1995, 1999, 2008, 2012). On fields with initially low to moderate populations of *P. thornei*, chickpea has been used as a susceptible noncereal crop to amplify RLN density without also amplifying inoculum of fungal pathogens that attack wheat. On fields with moderate to high initial RLN density, fallow or crops of sorghum or resistant wheat cultivars have been used to reduce the density of *Pratylenchus* in adjacent strips or blocks. A more rapid option has been to apply strips of aldicarb nematicide to infested fields at the time of planting (Smiley 2009a; Smiley et al. 2005b, c, 2014a; Taylor et al. 1999; Thompson and Clewett 2021a; Thompson et al. 1995, 2012).

Newer methods have been developed to differentiate tolerances among large numbers of cultivars and breeding lines planted into RLN-infested soils in Australia. Both methods are conducted without the need to manipulate native RLN populations by applying a nematicide during the test year, or by planting resistant or susceptible crops prior to the test year. One method involves a leaf and plant chlorosis rating system (Thompson et al. 1999). A more quantitative assessment of tolerance was recently also reported by Thompson et al. (2021). They applied a multiple components analysis to evaluate cultivars for tolerance in multiple trials in which the only measured parameters were grain yield and the initial nematode density over the trial area. The analysis compared grain yields for 29 field experiments conducted on infested fields during different years and at different locations. The analysis accounted for 84% of the genotype-experiment variance and covariance for the 784 wheat genotypes evaluated. Thompson et al. (2021) also established and validated a quantitative tolerance index to predict relative grain yield of wheat genotypes on soils infested by *P. thornei*. The nine-point rating scale with arithmetically equal categories distinguished among genotype tolerance traits. For each of the nine categories, a range of grain yields was predicted and a commercial cultivar was designated as the specific reference genotype for future experiments. The report by Thompson et al. (2021) also distinguished two components of tolerance. A tolerance component associated with a genotype's ability to restrict reproduction of *P. thornei* (e.g., resistance) (Thompson et al. 2020) was designated as general tolerance. A tolerance component independent of the genotype's resistance was designated as specific tolerance or specific intolerance. Wheat cultivars exhibiting tolerance to *P. neglectus* and *P. thornei* have been deployed effectively in Australia but tolerance alone was not considered an effective long-term management strategy. Planting tolerant but susceptible cultivars enables the nematode to multiply into damaging densities that pose a threat to a subsequent intolerant crop (Thompson et al. 1999, 2008, 2021; Vanstone et al. 1998, 2008). In the PNW, studies of RLN tolerance in wheat were very limited (Smiley 2009a; Smiley et al. 2014a) and have not been sustained. The new analytic tools described by Thompson et al. (2021) will become invaluable for evaluating future yield trials in the United States.

Planting date. Yield of irrigated wheat in *P. thornei*-infested fields in Mexico was improved by delaying planting by 1 month (Van Gundy et al. 1974). This response was attributed to seedlings overwintering with lower populations than for earlier plantings of larger plants. It appears possible that this strategy could also be

applied in the PNW. Winter wheat in cultivated wheat-fallow rotation is planted as early as possible during late summer or early autumn. This is accomplished using a deep-furrow drill to place wheat seed into moist soil 2 to 3 cm below an air-dry layer of fallow. This practice allows for vigorous establishment of wheat stands before seed of winter-annual weeds germinate and before the onset of winter dormancy (Schillinger et al. 2006). However, planting winter wheat into nontilled fallow is becoming more widespread. No-till fallow seldom retains sufficient moisture close enough to the surface to allow even deep-furrow drills to place wheat seed into soil moist enough to germinate the seed. Therefore, no-till plantings using shallow seed openers are usually made shortly before or after a soaking rain, which often occurs during late autumn. No-till plantings are usually made one or more months after winter wheat is planted into cultivated fallow (Williams and Wuest 2021). Soil at planting depth is usually much colder when wheat is planted into no-till than into cultivated fallow (Fig. 2). The difference in planting date and soil temperature should be investigated to determine its effect on nematode invasion. Thompson (1992) reported that higher population densities of *P. thornei* occurred at shallow depths in no-till than in cultivated fields.

Trap and biofumigant crops. The use of trap or biofumigant crops is precluded in PNW dryland agriculture by the critical need to preserve as much stored water as possible for use by the profit-generating winter wheat crop. Potential biofumigant crops such as sudan grass and cruciferous oilseed crops within the Brassicaceae family are grown on only small amounts of land in the low- and intermediate-precipitation zones. Those crops are grown to maturity and are harvested for seed. Under that production system, populations of RLNs may increase or remain high (Smiley et al. 2008a, 2014b).

Green-manure crops are used to sanitize soil through biofumigation in regions where water is not the most limiting factor for wheat growth. When green tissue of some of these crops is macerated and incorporated into soil, toxic products are produced that reduce the density of *Pratylenchus* spp. (Bernard and Montgomery-Dee 1993; Forge et al. 2000; Potter et al. 1998, 1999). Potter et al. (1998) reported that *P. neglectus* was suppressed much more by macerated leaf tissue of *Brassica* spp. (56 to 95%) than by root tissue (0 to 48%). Within roots, the suppressive influence was correlated with the concentration of 2-phenyl glucosinolate, with roots of some *Brassica* spp. and cultivars being more suppressive than for other species or cultivars. Relationships between *Pratylenchus* spp. and cruciferous oilseed crops are complex. It is unlikely that biofumigant crops or seed meals will become useful for managing RLNs on vast tracts of dryland wheat.

Weed control. One or both *Pratylenchus* spp. reproduce on most grass and broadleaf weeds common to dryland agricultural regions of the PNW (Fig. 17) (Smiley et al. 2014c). In winter wheat-fallow rotations, volunteer cereals and winter annual grass weeds often emerge in wheat stubble and grow for 4 to 5 months from early autumn until they are killed in the spring. Although reproduction of RLNs is slowed by cold winter temperature, there is sufficient time at which soil temperature is above the minimum (8°C) for invasion and multiplication of *Pratylenchus* spp., especially at greater depths of the soil profile. These overwintering hosts enable RLN densities to increase on volunteer wheat and susceptible weeds. Therefore, the presence of living plants during the fallow “sanitation” phase converts a 2-year winter wheat-fallow into an annual RLN-host-plant system, and an annual spring cropping system into a year-long “double-crop” host system. Control of weeds and volunteer cereals during the fallow phase of a wheat-fallow rotation is as important as it is during the in-crop phase.

Reproduction of *P. thornei* on downy brome and of both *P. neglectus* and *P. thornei* on jointed goatgrass (Smiley et al. 2014c) pose the potential for additional concern when fields infested by these weeds are planted with a winter wheat cultivar that carries resistance to an imazamox or quizalofop herbicide (Lyon et al. 2020). Herbicide-resistant wheat cultivars are planted to facilitate the selective killing of weeds by applying the appropriate herbicide over an entire wheat crop canopy. If RLNs have colonized roots of a weed grass as well as volunteer and planted wheat, the nematodes are afforded an opportunity to migrate from dying weed and volunteer wheat roots to nearby roots of herbicide-resistant wheat. Thus,

the killing of the weeds and volunteer hosts can encourage further concentration of RLNs in the intended wheat crop. This must be considered among possible explanations for instances where a herbicide-resistant cultivar fails to produce as much grain as was anticipated after competing weeds were removed.

Crop nutrition and supplemental irrigation. Thompson and Clewett (2021a) demonstrated that *P. thornei* reduced uptake of nitrogen and phosphorus, leading to suppressed growth and yield of wheat. Addition of fertilizer improved grain yield during a wetter but not a drier year. However, when soil was treated with aldicarb, grain yields were improved where crops were also fertilized, especially during the drier year. Addition of additional fertilizer is not an option in the PNW, where the market class of low-protein soft white wheat is fertilized as minimally as possible to attain high yield as well as low protein content.

RLNs also induce premature drought and reduce yield by impeding the uptake of stored soil water that would be available for use by healthy plants (Smiley and Machado 2009; Thompson et al. 1995; Whish et al. 2014). The economic threshold for damage by *P. neglectus* and *P. thornei* is lower in low-rainfall environments than in crops produced in irrigated crops or areas of greater precipitation (Castillo et al. 1995; Nicol and Ortiz-Monasterio 2004; Orion et al. 1984). Although crop damage can be minimized by supplying additional nutrients nutrition and water, these inputs are not possible during the in-crop phase of dryland wheat-fallow rotations in the PNW.

Chemical and biological nematicides. Although no chemical or biological nematicide is currently available to restrict RLN damage in dryland wheat, methods to amplify the efficiency of these nematicides are being pursued by manufacturers.

Chemical nematicides are effective but are not registered, not economically feasible, or not environmentally appropriate for managing these parasites on large areas of lower-value nonirrigated field crops. Biological nematicides are not yet effective for increasing yields of wheat in *Pratylenchus*-infested fields in the PNW. Formulations of avermectins and the bacterium *Bacillus firmus* were ineffective as seed treatments (Smiley et al. 2012). *Pasteuria thornei*, a host-specific obligate bacterial endospore-forming parasite of *Pratylenchus* spp. (Starr and Sayre 1988), is present in PNW dryland fields and is effective as a seed treatment on soybean in greenhouse assays (Confort and Inomoto 2018). However, greenhouse pots do not represent field conditions, where roots expand far beyond the treated zone. Öztürk et al. (2020) reported that *Pratylenchus thornei* in Turkey contained far more numbers of attached *Pasteuria* spp. than were present on *P. neglectus*. Although a survey of *Pasteuria* on *Pratylenchus* spp. has not been conducted in the PNW, wheat grain yield is significantly reduced by RLNs in fields where native populations of *Pasteuria* attached to *P. thornei* have been observed (Smiley et al. 2005b).

As a research tool, aldicarb is effective for assessing RLN damage on short-season crops, and has the added advantage of not significantly affecting other monitored components of the soil microflora and microfauna (Doyle et al. 1987; Kimpinski and Johnston 1995; Smiley 2009a; Smiley et al. 2005b, c, 2014a; Taylor et al. 1999; Thompson and Clewett 2021a; Thompson et al. 1995, 2012). Aldicarb suppresses RLN populations only at shallow depths in heavier soils (Doyle et al. 1987; Thompson and Clewett 2021a), and dissipates too rapidly to protect winter wheat roots during the spring (Smiley 2009a). Growth of even one susceptible crop after aldicarb treatment allows high RLN populations to become reestablished.

Other management strategies. The effect of tillage and fallow on RLNs is unclear. Reports that cultivated fallow reduces populations of *P. neglectus* and *P. thornei* (Nombela et al. 1998; Orion et al. 1984; Smiley et al. 2004b; Strausbaugh et al. 2004; Thompson 1992) were based upon soil samples collected to much shallower depths than those at which these nematodes often attain peak density (Ophel-Keller et al. 2008; Smiley et al. 2008a; Taylor and Evans 1998; Thompson et al. 1999).

Outlook for PNW Dryland Agriculture

Climate models project a 10% increase in annual precipitation for dryland agricultural areas of the PNW during the next 50 years (Karimi et al. 2018). Mean temperature is projected to increase by

2°C during the winter wheat growing season but will not change for spring grains because they will be planted earlier than at present. Increasing carbon dioxide is projected to counterbalance warming and to increase wheat yields until midcentury but the effect on yield is expected to decline thereafter. The increasing carbon dioxide will purportedly increase the transpiration-use efficiency, which will increase wheat yields by 18 to 48% in the PNW low- and intermediate-precipitation zones during the next five decades (Karimi et al. 2017). These changes in climate and wheat productivity are projected to cause a decline of winter wheat-fallow by at least 10%, with a commensurate increase of annual cropping. Other winter crops are being suggested as possible diversifications available for areas currently planted only to winter wheat (Stöckle et al. 2018). Additional research is necessary to predict impacts of increasing crop intensity on diseases caused by soilborne plant pathogens.

Agriculture in the PNW consists of a mixture of irrigated and dryland production. Irrigated lands occupy 3.3 million ha (7.3 million acres), for which water is derived from groundwater or rivers (CAST 1996). About 10% of irrigated land is used to produce wheat or barley. Groundwater and surface resources in the PNW are already fully committed.

Some land previously irrigated from groundwater is already being permanently shifted to dryland agriculture due to declining aquifer levels, increasing energy costs, and the ability of other water users to bid water rights away from agriculture. Small-grain and forage crops are of lower value than most other irrigated crops, and grain crops can be profitably produced without irrigation. Therefore, grains and forages are the first crops to be eliminated or restricted when groundwater shortages occur or are anticipated.

In the western United States, mountain snow is responsible for 70% of water flowing in rivers and streams (Li et al. 2017). These authors projected that, by 2100, the contribution of snowmelt to runoff will decrease by one-third. During past decades the snowpack did decline and melt sooner, and those trends were accompanied by stronger and more frequent hydrologic extremes. Dams in major rivers were constructed for climates of many decades ago. Currently, water must be released earlier due to flood control requirements and a finite reservoir storage capacity. That has reduced warm-season streamflow but also required additional drawdowns of reservoirs to maintain minimum temperatures for migrating fish. Any seasonal increase in demand for one essential use of surface water (hydroelectric generation, migration of anadromous fish, barge navigation, recreation, or crop production) requires a diminished allocation for another use. Water allocations are already restricted for some irrigated land during periods of low stream flow and years of drought.

Future Research Needs for Lesion Nematodes

Additional regional research is needed for all aspects of crop genetics, with a special focus and source of dedicated funding for screening wheat for genetic resistance and tolerance. However, crop genetics alone may not succeed in achieving a level of desired RLN management. Emphasis is also needed for enhanced nematode testing of fields and more efficient communications relating to their impact. Studies are also needed on all aspects of *Pratylenchus* biology, including mechanisms of resistance and the phytobiome, and the role of changing climates on the dryland cropping systems and impacts on productivity by root and crown diseases. Discussion of these research topics are expanded in the following sections.

Crop genetics. Resistance breeding could be expedited by developing additional molecular markers to assist with introgression of RLN resistance into commercial cultivars (Okubara et al. 2019). Although there is currently no research to identify wheat cultivars with tolerance to RLNs, this need appears to be performed surreptitiously during statewide cultivar testing programs, where traits such as stripe rust resistance and grain yield and test weight are quantified at many locations each year. In the only dedicated screening for tolerance conducted thus far, the average *Pratylenchus* tolerance for a group of commercial wheat cultivars was much higher than for a group of advanced breeding lines (Smiley 2009a). The majority of lines that became registered as cultivars appeared to have been

selected for improved tolerance to *Pratylenchus*, even though that was not a trait scored in statewide tests.

There is a need to develop a recurring funding avenue that assures an ability to routinely characterize resistance and tolerance traits in current cultivars and advanced breeding lines of wheat and potential rotation crops. Very little testing is being conducted in the PNW, and funds for such services are currently available mostly from commodity commissions that allocate funds on an annual basis according to the competitive merit of annual proposals.

In contrast, Australian scientists and the grains industry have been engaged in RLN research for more than 50 years, making that country the international leader in study of this pathogen on wheat and other field crops. More than 60% of Australian wheat cultivars now possess moderate to high levels of tolerance to *P. thornei* (Simpfendorfer et al. 2019). This achievement is the result of rigorous testing of wheat cultivars for resistance and tolerance every year. Annual tests of tolerance to *P. thornei* have been conducted for all commercial cultivars and advanced breeding lines for more than two decades (Thompson et al. 2021). Advanced breeding lines are screened for RLN tolerance 3 years before they can be registered as cultivars (Thompson et al. 1999). Screenings for tolerance are accompanied by screenings of breeding lines and cultivars to identify sources of resistance (Sheedy and Thompson 2009; Thompson et al. 2020). These tests are funded by the National Variety Testing program of the Grains Research and Development Corporation (GRDC) (<https://grdc.com.au/>). The GRDC publishes newsletters and crop sowing guides to actively communicate results of resistance and tolerance tests to agronomists, plant breeding companies, and growers. Australian public-sector prebreeding programs are also formally linked to commercial breeding companies and to international programs at the International Center for Agricultural Research in the Dry Areas and CIMMYT. The domestic and international prebreeding programs identify, develop, and deploy germplasm with high levels of resistance and tolerance to RLNs and other soilborne pathogens (Nicol et al. 2007). Although breeding wheat for resistance to either *P. neglectus* or *P. thornei* is occurring in several PNW states, it appears likely that multinational breeding companies will be the first to introduce wheat cultivars with resistance and tolerance to *Pratylenchus* spp. into the United States.

Nematode testing and communication. Some commercial nematology laboratories in the PNW offer a service in which DNA is extracted from soil to distinguish and enumerate important nematodes and plant-pathogenic fungi (Smiley 2015b). Those and most other labs previously counted *Pratylenchus* spp. using morphological characteristics but were reluctant or would not identify species. However, a relatively small proportion of samples for DNA analysis are submitted from dryland field crops. Because commercial testing of nematodes in dryland agriculture is very limited in the PNW, the true impact of RLNs on wheat yield and profitability is considered to be poorly documented and likely estimated far too conservatively.

A robust soilborne disease testing program, similar to that for dryland agriculture in Australia, is needed in the PNW. Australian cultivar improvement programs are supported by a national DNA-based testing program that identifies risks from soilborne plant-pathogenic fungi and plant-parasitic nematodes affecting broadacre field crops (Ophel-Keller et al. 2008). The Predicta B soil testing service processes thousands of samples annually to estimate risks from losses due to diseases of roots and lower stems (https://www.pir.sa.gov.au/research/services/molecular_diagnostics/predicta_b). The testing service established data that allows agronomists to use results of molecular tests to define for farmers an estimate of disease risk and potential crop loss. In the PNW, data are not sufficient to develop a quantitative estimate of risk for crop damage by measuring nematode DNA in soil.

***Pratylenchus* biology.** Populations of *P. neglectus* and *P. thornei* have not been evaluated for pathotypic specialization in dryland regions of the PNW. The presence of differential hosting preferences for *P. neglectus* populations on other crops in the western United States (Al-Khafaji et al. 2019; Griffin 1991; Hafez et al. 1999) suggests that this possibility may also exist for wheat. The potential for existence of *P. thornei* pathotypes in Turkey was recently suggested

by Goze Ozdemir (2021). Screening tests are required to evaluate these possibilities and potential implications for wheat breeding and for crop management in the PNW.

Mechanisms of resistance. Root structural and architectural components need to be evaluated as a potential means for increasing resistance to root penetration or migration by RLNs. Resistant genotypes in an RLN-resistance mapping population had greater root lignin content (Thompson et al. 2015) and distribution of lignin to the outermost cells (Thompson et al. 2017). The RLN-resistant landrace wheat parent impeded multiplication of *Pratylenchus* spp. (Sheedy et al. 2007; Smiley et al. 2008b, c, d) and reduced the population density of RLNs in the field (Smiley et al. 2014a). The mapping population also segregated for resistance to at least four soilborne pathogens: *P. neglectus*, *P. thornei*, *F. culmorum*, and *R. solani* AG-8 (Thompson et al. 2017).

Rahaman et al. (2020) reported both higher constitutive (existing) levels of phenols in wheat genotypes resistant to *P. thornei* as well as induction of greater polyphenol oxidase and peroxidase enzymes in resistant than susceptible genotypes. These phenolic compounds and inducing enzymes are in biochemical pathways leading to complex phenol polymers such as lignin. Likewise, Schneider et al. (2021) demonstrated that wheat roots which were most capable of penetrating restrictive layers of soil contained multiseriate cortical sclerenchyma (MCS). Roots with that structural feature had a greater lignin content and greater cell wall-to-lumen ratio in outer cortical cells. Plants with MCS produced a greater root biomass at greater depth, enabling them to better withstand edaphic stress. It appears important to determine whether MCS is a component of observations for RLN-resistant wheat reported by Thompson et al. (2015, 2017). Nevertheless, regulation of lignin biosynthesis as a nematode management strategy will undoubtedly face complexities associated with the multifaceted roles of lignin in plants (Xie et al. 2018).

Linsell et al. (2014b) also evaluated mechanisms of resistance to *P. thornei*. The nematode was equally attracted to and penetrated roots of both resistant and susceptible wheats. In resistant wheat, the rates of migration, juvenile maturation, egg hatch, and egg deposition were suppressed, suggesting a constitutively expressed resistance mechanism. Resistant wheat was fully susceptible to invasion but allowed less than 10% of invading individuals to develop into the adult stage. Similar processes were suggested for resistance to *P. neglectus*. As discussed earlier, the benzoxazinoid group of secondary metabolites are associated with *Pratylenchus* resistance in wheat (Frew et al. 2018). In maize, these compounds selectively enhanced (*P. neglectus*) or repressed (*P. crenatus*) reproduction of different taxa within the genus *Pratylenchus* (Sikder et al. 2021). These complex relationships warrant further research in wheat.

Plant responses to abiotic and biotic stresses are often closely associated. Much progress has been made toward understanding abiotic stress mechanisms in wheat and other crops (Kumar et al. 2020, Shinwari et al. 2020), and should be expanded to research on tolerance to RLNs.

There is a strong need for further research on molecular approaches toward understanding and manipulating the interaction between RLNs and their hosts. Topics of special importance for RLNs include the roles of effectors, gene silencing, and plant transformations, many of which were reviewed by Jones and Fosu-Nyarko (2014) and Smiley et al. (2017). The following synopses are abbreviated from Smiley et al. (2017).

Effectors or genes encoding them are required for successful nematode parasitism (Hogenhout et al. 2009). Effectors are small molecules such as proteins or peptides that can modify the structure or physiology of host cells to allow a nematode to overcome host defense. Effectors are developed in the nematode and are inserted into a host plant cell through the stylet (Mitchum et al. 2013). Jones and Fosu-Nyarko (2014) presented a summary of *Pratylenchus* spp. proteins and effectors secreted into plants, as arranged by functional groups of cell-wall-modifying enzymes, protection from host defense, targeting regulation and signaling pathways, feeding, and unknown functions. Studies are being conducted to advance understanding of the mode of action of effectors and whether they can be managed to control nematodes.

Traditional breeding programs require the screening of great numbers of genotypes to identify useful resistance genes. After being identified, those genes must be incorporated into agronomically adapted cultivars through many generations of crosses and repeated screenings. Although marker-assisted selection has shortened that process, the use of transgenic plants presents an alternative strategy for developing resistant plants, either by transferring functional resistance genes directly, or by developing “synthetic” resistance genes which are ingested by feeding nematodes and then interfere with vital processes in the nematode-plant interaction (Samac and Smigocki 2003; Tan et al. 2013).

Host-induced gene silencing (HIGS) studies are being conducted with transgenic plants to measure changes in the expression of targeted genes and to evaluate the effects of gene silencing on features such as nematode attraction, migration to roots, motility, reproduction, and behavior (Dutta et al. 2015; Fosu-Nyarko and Jones 2016; Tan et al. 2013). However, reducing the expression of plant genes involved in the nematode-plant interaction is often found to be detrimental to crop plants because the silenced plant genes have functional roles that, when silenced, can reduce field performance.

The technical complexity, expense, and social constraints for developing transgenic crops are enormous. These issues can be bypassed by delivering double-stranded RNA as a foliar spray that becomes systemically translocated downward into roots, whereupon it is ingested by the feeding nematode (Fosu-Nyarko and Jones 2016). This novel gene-silencing technology is promising for development of genome-enabled chemical nematicides (Danchin et al. 2013; Fosu-Nyarko and Jones 2016).

Another transgenic approach involves expression of an antifeedant cysteine proteinase inhibitor in plants to interfere with nematode digestion, and an antiroot invasion nonlethal synthetic peptide (Atkinson et al. 2004; Tripathi et al. 2015). Cysteine proteinases are major digestive enzymes of many nematodes. Small protein inhibitors (cystatins) from plants have mediated nematode resistance when expressed in several crops. Cystatin is a small peptide that is a normal part of the human diet and does not pose a biosafety or environmental concern (Tripathi et al. 2015).

Genome editing is an alternative to RNA interference for silencing genes. It involves a targeted mutation induced in a nontransgenic manner, or the insertion of oligonucleotide sequences. The use of an RNA sequence to direct a dsDNAse enzyme (CRISPR-Cas9) to cut a target sequence at a specific site is now the most widely used genome editing process (Dutta et al. 2021; Lozano-Juste and Cutler 2014). However, whereas, in HIGS, the silencing trigger is delivered from the plant to the pest, it is not yet possible to deliver a nontransgenic genome editing signal by editing the genome. To apply this technology, it will be necessary to find and edit to become nonfunctional a nonvital host plant gene whose expression is needed for nematode parasitism. Descriptions of whole-genome sequences for wheat and barley could expedite the development of nontransgenic genome-edited cereals with resistance to RLNs.

The phytobiome. Great emphasis during the past century was directed to studies of interactions among plant roots, soilborne plant pathogens, and other soil microbes. Those studies included bacteria, archaea, fungi, animals, viruses, and soil enzymes that interact with and influence plants and pathogens (Baker and Cook 1974; Dommergues and Krupa 1978; Foster et al. 1983; Hornby 1990; Krasil'nikov 1968; Krupa and Dommergues 1979; Lynch 1983). Studies of these microbial and plant-microbe interactions now involve advanced technologies and were renamed as studies of the “microbiome” or “phytobiome” (CAST 2020; Leach et al. 2017; Phytobiomes 2016). Components of a phytobiome are described to include interactions among crops, individual plants, microorganisms (viruses, bacteria, fungi, oomycetes, and algae), animals (arthropods, worms, nematodes, and rodents), and physical and chemical environments of soil, air, water, and climate. Interactions among these components are clearly dynamic and complex. The hope of the phytobiome concept is to use a systems approach to create understandings of all components and interactions, with an ultimate goal to shift agricultural production from a focus on managing individual components to managing the entire system as a single entity. Advanced technologies are being

developed to coordinate and interpret the vast amounts of information currently being generated by new DNA-based sequencing technologies for identifying organisms present in phytobiomes.

Dryland agricultural systems. Dryland agriculture in the PNW will continue to evolve (Cann et al. 2020; Stöckle et al. 2018), will become increasingly important, and will remain strongly focused on production of winter wheat. There is great need and economic justification for additional research to combat chronic and acute damage caused by root and crown diseases in dryland cropping systems (Paulitz et al. 2002; Smiley 1996, 2009a; Smiley et al. 2013b, 2016). In the low- and moderate-precipitation zones alone, just two diseases caused by soilborne pathogens cost growers an estimated \$64 million annually from lost production opportunities: \$51 million from root-lesion nematodes (Smiley 2009a) and \$13 million from *Fusarium* crown rot (Smiley et al. 2005a). In the high-precipitation zone and in irrigated agriculture, growers lose another \$77 million annually from take-all root rot (Folwell et al. 1991) and \$3 million from cereal cyst nematodes (Smiley 2009b). Estimates of losses are not available for important and chronic root diseases caused by species of *Pythium* and *Rhizoctonia*.

It would appear that the time has arrived in the PNW to shift primary funding emphasis from a now-controllable foliar disease (stripe rust) to the still-difficult and highly damaging root and crown diseases caused by soilborne pathogens. There is little or no crop loss when fungicides are applied to control stripe rust (Chen 2020). This is achieved through deployment of resistant cultivars, scouting fields, and applying fungicides as needed. The average annual expense to control stripe rust with fungicides is \$10 million across the entire region (Chen 2020). That expense is far less than the estimated \$144 million of lost profitability caused collectively by just four root and crown diseases (*Fusarium* crown rot, take-all, root-lesion nematodes, and cereal cyst nematodes). The hypothetical loss of winter wheat yield if fungicides were not applied to control stripe rust in the PNW would average 533 kg/ha/year (7.5 bushels/acre/year) across the 566,118 ha (1.4 million acres) of winter wheat (Chen 2014). That loss equates to 301,740 metric tons (= 8.1 million bushels) which, at a market price of \$243/metric ton (\$6.00/bushel), represents an annual loss of \$73.3 million for unprotected winter wheat. The additional hypothetical loss from stripe rust on unprotected spring wheat would average 578 kg/ha/year (8.1 bushels/acre/year) for 141,152 ha (349,000 acres) (Chen 2014). That loss would equate to 81,586 metric tons (= 3 million bushels), which represents an annual loss of \$19.8 million for unprotected spring wheat. Thus, when fungicides are not applied, losses from the only foliar disease of economic significance in the region is estimated to reduce annual profitability by about \$93 million. However, in reality, almost all wheat in the region is treated with a prophylactic fungicide when necessary, resulting in little or no economic loss other than for costs of fungicide and application.

Conclusion

During the past two decades, much has been learned about the biology and control of RLNs in PNW dryland agricultural systems. Many additional challenges regarding expanding that understanding were identified in this treatise. A particularly critical challenge will be to develop dedicated scientific positions and sustained funding to screen cultivars and breeding lines of dryland field crops for resistance and tolerance, and to transmit that information to growers, agronomists, and plant breeders, as has been successfully implemented and maintained in Australia.

Globally, great emphasis has focused on identifying and minimizing the difference between actual and potentially attainable yields for many crops (FAO 2015; Hatfield and Beres 2019). The so-called “yield gap” is greater for rainfed than irrigated crops and, for rainfed wheat, the yield gap has remained static as actual yields have increased. Seasonal distributions and amounts of rainfall during the growing season are suggested as the primary reason for the yield gap in rainfed wheat. Lesser contributing factors include those that affect seasonal evaporation such as tillage, stubble management, row spacing, and rates of canopy fill and senescence. Therefore, nearly all studies identify water-use efficiency as the most limiting factor restricting crops from reaching their full yield potential given the total amount of

water available. Recognition is seldom given to impacts of nematodes and fungal pathogens that greatly reduce water-use efficiency over vast areas of cropland. An exception was recognition of the role of *Rhizoctonia* root rot in reducing water-use efficiency of rainfed wheat in Australia (FAO 2015). The yield gap for rainfed wheat in the PNW cannot be effectively reduced without particular recognition of the roles of two chronic and severe diseases (root-lesion nematodes and *Fusarium* crown rot) which each greatly suppress the ability of plants to transmit plant-available stored water from roots to foliage. Further definition of the role of RLNs will require appointment of applied scientists responsible for addressing crop genetics and communicating associated information identified in this section.

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Richard W. Smiley

Richard W. Smiley earned a B.Sc. degree in soil science at the California Polytechnic State University (San Luis Obispo, CA), and an M.Sc. degree in soils and Ph.D. degree in plant pathology at Washington State University. He was employed as an Assistant Soil Scientist (USDA-Agricultural Research Service, Pullman, WA), Research Soil Microbiologist (Commonwealth Scientific and Industrial Research Organization, Adelaide, Australia), and Assistant and Associate Professor of Plant Pathology (Cornell University, Ithaca, NY). In 1985, he became Director of Oregon State University's Columbia Basin Agricultural Research Center, where he was also a Professor in the Department of Botany and Plant Pathology at Oregon State University. He administered research stations at Pendleton and Moro, OR and conducted research and extension on etiology and management of soilborne plant-pathogenic fungi and plant-parasitic nematodes, with a focus on root diseases of wheat and barley. He held service and leadership roles in The American Phytopathological Society, Council for Agricultural Science and Technology, International Society of Plant Pathology, and other organizations, including service as Editor-in-Chief of APS Press. After retiring in 2015, he continues to report unpublished research and serve on international and community boards, and has published centennial histories for agricultural research in eastern Oregon, and for the Rotary Club of Pendleton. E-mail: richard.smiley@oregonstate.edu

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