DISSEMINATION OF THE STEM AND BULB INFESTING NEMATODE, TYLENCHUS DIPSACI, IN THE SEEDS OF CERTAIN COMPOSITES

By G. H. Godfrey,
Pathologist, Office of Cotton, Truck, and Forage Crop Disease Investigations, Bureau of Plant Industry, United States Department of Agriculture

The investigations recounted in this paper were carried on as a result of the finding of the widespread occurrence of the stem-nematode-infested false dandelion, Hypochaeris radicata, in the Pacific Coast States, as reported by Godfrey and McKay (#). My subsequent discovery of the same nematode in the true dandelion, Taraxacum officinale, over a wide area in northeastern United States in July and September, 1923, made the problem of the manner of dissemination the more interesting.

REVIEW OF LITERATURE

A study of the literature has shown that both of these hosts are more or less abundantly infested by nematodes in Europe, as indicated by their frequent mention by writers on plant galls. In 1885 Trail (19, p. 211) listed Hypochaeris radicata as subject to a gall caused by Tylenchus sp. He reported observing it first in Scotland, in 1882. This seems to be the earliest authentic report. In 1886 Liebel (6, p. 573, No. 288) listed it as subject to a "Helminthocecidium" in Italy, described the symptoms, and illustrated with drawings typical affected leaves and stems, identical in appearance with the disease produced in this country by Tylenchus dipsaci (Kühn) Bast. Thus this plant is reported all the way from Scotland to Italy as subject to galls produced by nematodes, it seems safe to assume by T. dipsaci.

The true dandelion, Taraxacum officinale, was mentioned by Thomas in 1885 (16) as subject to a "Helminthocecidium," and more completely described the next year (16, p. 304, No. 49). The causal organism was referred to as Tylenchus sp. in a still later paper (17). It was found, in this instance, in "Größter Menge auf den Wiesen um Cogne, Gimilian und Lillian, Piémont, bei 1,500 to 1,800 m. Meereshöhe." Liebel (6, p. 573, No. 288), in 1886, reported a "Helminthocecidium" on this host at Bolchen, Lorraine. Rübsaamen reported it in 1890 (13, p. 53, No. 207) in "Die Gallmücken und Galle des Siegerlandes." Houard (3, p. 1042, No. 6037) lists it for northern, central, and southern Europe as a Tylenchus gall. With Taraxacum again, though the specific parasite is not named, Tylenchus dipsaci is strongly indicated in every case.

1 Received for publication Mar. 20, 1924.
2 Reference is made by number (italic) to "Literature cited," p. 478.
3 I gratefully acknowledge my indebtedness to Dr. G. Steiner, Office of Crop Technology, Bureau of Plant Industry, for his help in finding the pertinent European literature.
European writers report various other composites as subject to nematode galls, most of which, judging from the descriptions given (except the root galls) are probably due to *Tylenchus dipsaci*. These are tabulated herewith:

**Table I.—Composite plants subject to Nematode galls**

<table>
<thead>
<tr>
<th>Host plant</th>
<th>Nematode as listed</th>
<th>Date</th>
<th>Authority</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>Atractylis gummifera</em> L.</td>
<td>do</td>
<td>1912</td>
<td>Do.</td>
</tr>
<tr>
<td><em>Carduus defloratus</em> L.</td>
<td>Tylenchus sp.</td>
<td>1896</td>
<td>Thomas (18).</td>
</tr>
<tr>
<td><em>Carpina corymbosa</em> L.</td>
<td>do</td>
<td>1909</td>
<td>Houard (3).</td>
</tr>
<tr>
<td><em>Cichorium intybus</em> L.</td>
<td>Anguillulidae</td>
<td>1902</td>
<td>Geisenheyn (1).</td>
</tr>
<tr>
<td><em>Cirsium oleraceum</em> (L) Scop.</td>
<td>do</td>
<td>1896</td>
<td>Thomas (18).</td>
</tr>
<tr>
<td><em>Cirsium oleraceum</em> (L) Scal.</td>
<td>Tylenchus sp.</td>
<td>1902</td>
<td>Geisenheyn (1).</td>
</tr>
<tr>
<td><em>Cirsium arense</em> (L) Scal.</td>
<td>do</td>
<td>1902</td>
<td>Do.</td>
</tr>
<tr>
<td><em>Cirsium bulbosum</em> (Lam.) DC</td>
<td>do</td>
<td>1912</td>
<td>Houard (3).</td>
</tr>
<tr>
<td><em>Crepis foetida</em> All.</td>
<td>Tylenchus sp.</td>
<td>1905</td>
<td>Trotter (80).</td>
</tr>
<tr>
<td><em>Crepis taraxacifoia</em> Thuill.</td>
<td>Tylenchus devastatrix</td>
<td>1896</td>
<td>Maige (8).</td>
</tr>
<tr>
<td><em>Cynara cardunculus</em> L.</td>
<td>Tylenchus dipsaci.</td>
<td>1912</td>
<td>Stefani Perez (14).</td>
</tr>
<tr>
<td><em>Hieracium auricula</em> L.</td>
<td>do</td>
<td>1903</td>
<td>Lagerheim (see Houard (5)).</td>
</tr>
<tr>
<td><em>Hieracium pilosella</em> L.</td>
<td>do</td>
<td>1883</td>
<td>Traill (19).</td>
</tr>
<tr>
<td><em>Leontodon bastili L.</em></td>
<td>Anguillulidae</td>
<td>1885</td>
<td>Liebel (6) and several others.</td>
</tr>
<tr>
<td><em>Leontodon hispidus</em> L.</td>
<td>Tylenchus sp.</td>
<td>1907</td>
<td>Mariani (see Houard (5)).</td>
</tr>
<tr>
<td><em>Leontodon incanus</em> Schrank</td>
<td>Anguillulidae</td>
<td>1896</td>
<td>Do.</td>
</tr>
<tr>
<td><em>Leontodon pyrenaeus</em> Guan</td>
<td>Tylenchus sp.</td>
<td>1903</td>
<td>Lagerheim (see Houard (5)).</td>
</tr>
</tbody>
</table>

In only one of these cases, that of *Crepis taraxacifoia*, reported by Maige (8), was mention made of transmission of the nematode by seed. He described a condition of the flower head (capitule) very similar to that which occurs with the composites reported upon in this paper. He illustrated this condition with drawings, and treated of dissemination by the seed as follows:

*Les capitules attaqués portant des fruits d'apparence normale, bien que remplis de larves enkystées, ces fruits peuvent grâce a leurs aigrettes, être transportés par le vent à de grandes distances et constituent ainsi pour le *Tylenchus devastatrix* un moyen de propagation des plus favorables.*

The original paper on the stem nematode by Kühn (5) dealt with the organism in *Dipsacus fullonum* in the Dipsaceae, a family closely allied to the Compositae. Kühn wrote in this connection:

*DIESE Krankheit ist charakterisirt durch ein allmäliges Missfarbigwerden und Vertrocknen der Blüten-köpfe; Der Pappus des gesunden Samens ist gestielt, bei den kranken Körnern ist er fast doppelt so gross und sitzend. Die kranken Körner sind nicht vollständig mit Auguillulen ausgefüllt, vielmehr findet sich in denselben noch der verkümmerte Samenkern, während die ersteren zu weisslichen Häufchen vereinigt in dem Gewebe der abnorm verdickten Samenschale, namentlich am Grunde derselben vorhanden sind.*

Thus he established the presence of the nematodes within the seed head and seed of *Dipsacus fullonum*.

**DISTRIBUTION OF NEMATODE-INFESTED COMPOSITES IN AMERICA**

**HYPOCHAERIS RADICATA**

As stated in the paper by Godfrey and McKay (2), the stem nematode occurs along the west coast of America all the way from Tacoma, Wash., to San Francisco, Calif., in *Hyphaerais radicata*. This plant is reported to have been introduced into that region. In this regard Piper and Beattie (11) stated in their Flora of the Northwest Coast: "A very troublesome weed in lawns and pastures; introduced from Europe." Nelson (10) listed it as a possible introduction with ballast dirt. Mr. M. W. Gorman, botanist, now curator of the Portland Historical Society, at the Forestry Building, Portland, Ore., who is also familiar...
with ballast flora, considers this a very great probability. He is familiar with the early appearance of the plant in the Northwest, and with its very rapid spread and increase until now it is one of the most common and troublesome of lawn and meadow weeds. He referred me to Fort Nisqually, near Olympia, Wash., as the site of an early ballast dump, and the very possible point of introduction of the weed. True enough, in 1923 I found *Hypochaeris* in that vicinity in unusually great abundance as a roadside, lawn, and garden weed. Early settlers in that region stated to me that they knew when it first appeared, approximately 50 years ago.

The interesting observation was made as well, that the parasitic nematode *Tylenchus dipsaci* was observed to be very abundant in that region, possibly even more so than first observed in western Oregon, and certainly more abundant than in its southern range, in western California. It would appear to be very plausible to suppose that the parasite was introduced along with the host plant, and that the parasite as well as the host plant have become simultaneously widespread.

**CREPIS VIRENS**

While studying the flora associated with diseased *Hypochaeris*, I found a few typically affected plants of *Crepis virens*, first at Eureka, Calif., and later at Seaside, Oreg. They were by no means as abundant as affected *Hypochaeris radicata*, and merit attention only in the fact that they constitute a new host record for the organism.

**TARAXACUM OFFICINALE**

Stem-nematode-infested dandelions, *Taraxacum officinale*, were first encountered at Williamson, in Wayne County, N.Y., in July, 1923. Subsequently they were found occasionally all the way between Ithaca and Niagara Falls, and across the Niagara River, in the Province of Ontario, Canada. Plant disease survey forces in the State eventually reported the disease to be present in 14 counties in western New York. In September I found it among dandelions growing in a low meadow in Arnold Arboretum, in Boston, Mass.

With the true dandelion, therefore, as with the false dandelion in the West, considerable distribution of the parasite has taken place.

**RELATION OF THE NEMATODE TO THE SEED**

When first observations were made on nematode-diseased *Hypochaeris*, the plant was not flowering, consequently the disease was to be found only in the leaves. (2, Pl. 2). Later summer observations, however, disclosed the presence of swellings in the flower pedicels. The abundant occurrence of stem swellings due to an insect, *Aulax hypochaeridis* (Pl. 1, A) were at first confusing. Characteristic nematode swellings became evident, however, usually in the pedicel at the of the flower head. These were irregular, resulting sometimes in considerable distortion, and were distinctly soft, rather than hard as were the insect galls. Typical blossoms in this condition, compared with the normal, are shown in Plate 1, B and C. As stated previously, the swellings pictured by Massalongo (9) are identical in appearance with these.

Such affected stems of *Hypochaeris* when cut longitudinally showed brownish discoloration in the receptacle, and for a short distance below, in the pith of the stem. This condition is illustrated in Plate 1, D. The discolored tissue was found to contain an abundance of living, active *Tylenchus* in all stages of development.

Flowers in various stages of development were studied. By microscopic examination it was seen that some of the very young seed were discolored at their
point of attachment with the receptacle. These were found to contain nematodes. The eelworms could readily be seen with the binocular coiled up in the interior, through the semitransparent achene wall, as shown by Plate 2, A. Seeds in more advanced stages of development were found, upon dissection, to contain living nema. One showed a nema extending from the base. Another (Pl. 2, B) showed one at the upper extremity, at the base of the pappus stalk. Some of the seeds were killed by the invasion, as shown by their completely collapsed condition. In some of the invaded seeds, however, such injury did not occur, for the seed was intact, since the eelworms were present only between the achene wall and the testa of the seed.

Experimental plantings of seed from diseased flower heads produced a reduced stand of seedlings, among which were several typically diseased plants. Swellings appeared first in the petioles of the primary leaves, and subsequently in one or two of the permanent leaves. Plate 2, C, shows one of the affected seedlings with characteristic swelling in the midrib of the first secondary leaf. Examination of such a plant three days after infection was first evident disclosed larvae of Tylenchus dipsaci not yet quite sexually mature. In all invaded seed observed, the pappus was apparently normal and the seed capable of being transported by the wind. Plate 2, D, shows several mature seed of Hypochaeris radicata. Some of this same lot were later shown to contain living nema.

In the true dandelion (Taraxacum officinale) exactly the same conditions existed. The leaf symptoms are identical with those previously described for Hypochaeris radicata. Plate 3, C, shows typical leaf swellings. Plate 3, A, shows one of many nematode-infested heads found, this one sectioned to show the discolored receptacle and seed bases. More than 50 per cent of the seed in this particular head were invaded by nema. One of the seeds with its pappus is pictured in Plate 3, B. The seed is undamaged in spite of the fact that a nema-tode was present beneath the outer seed coat.

A study of growing plants made it evident how primary invasion of the seed head takes place. Both Taraxacum and Hypochaeris grow as a "rosette" on the ground, with flat leaves radiating from a common center. The outer ends of the leaves often are higher than the inner, thus permitting dew and rain to flow in toward the center, carrying with them free nema that have migrated out of infested spots in the leaves. Tylenchus dipsaci was thus observed many times in the young, actively growing central region of the plants, some of them free from the host tissues, others within the young, highly susceptible parts. Without doubt much of the leaf infection takes place when the leaves are young. It is likewise in this region that the flower heads form and develop. Ready infestation of the flower head can thus take place, and, indeed, many young heads were observed that were thus infested. Plate 3, D, a photograph of a dandelion plant sectioned longitudinally, shows two flower heads in different stages of development, and their obviously favorable location, when young, for infection by nema. The well-known rapid growth of the pedicel after the flower is fully open is a factor which favors the dissemination of the invading parasites, as well as of the seed, by the agency of the wind.

It is evident that dissemination of the nemas by the seed is easily accomplished, and under natural conditions it undoubtedly takes place to a large extent. If the seed has been killed, the eelworms released may still infest plants that are already established. If the infested seed is alive then a new colony is established at once, with the host plant immediately available. Thus is explained the distribution of the nematode parasite to an extent that is practically coequal in range with that of its host, the false dandelion, in the Pacific Coast States, and the probably widening circle of infestation in the true dandelion in the Northeast.
SEEDS OF OTHER PLANTS LIKewise NEMATODE CARRIERS

The dissemination of parasitic stem nematodes undoubtedly takes place by means of the seed of other composites and allied plants in a similar manner. Reference has already been made to the observations of Maige (8) in Crepis taraxacifolia. Geisenheyner (1) described a gall due to "Anguillulides" in Cirsium bulbosum in which the swelling is situated at the base of the flower head. (3, No. 5915, p. 1016), as it is in Hypochaeris and Taraxacum in America. A like condition exists with Leontodon incanus, in which the "Tige est épaissie et tordue, au-dessous de l'inflorescence, sur un longueur de 20 mm. et plus," etc., according to Houard (5, No. 6048, p. 1036). Likewise, in Hieracium pilosella "Capitule gonflé et contourné demeurant fermé, porté sur une hampe florale renflée." (Houard, 3, No. 1698, p. 1057). In all probability the seeds of all these plants are penetrated by the nemas, without injuring their capacity of being carried by the wind.

In Dipsacus fullonum, a member of the family Dipsacaceae, which is very close to the Compositae, the same manner of dissemination undoubtedly occurs, as already cited (5). Ritzema Bos (12) mentioned infestation in onion seedlings (Allium cepa) in the earliest stages of their development. A large part of this was due to the fact that penetration had taken place from infested soil shortly after the appearance of the cotyledon through the seed coat. In addition, however, he found Tylenchus dipsaci in the blossoms of mature plants, and in one case 3 per cent of the seeds were infested. In many other plants whose seeds are not windblown it is possible that the nemas enter the seed and are carried with them.

Dissemination of the plant parasitic nematodes on the surface of seed undoubtedly takes place to a large extent as well. This will be treated at length in another paper in connection with experimental work on the clover and alfalfa stem nematode.

SIGNIFICANCE OF WIND DISSEMINATION OF THE STEM NEMATODE

It is too early to make any estimate as to whether or not this great spread of the stem nematode in the composites may be of any economic significance. Indeed, any disease that even suggests the possible lessening of the spread of either the false or the true dandelion might be looked upon as a blessing rather than otherwise, except possibly in connection with the few fields of cultivated Taraxacum grown for food. Thus far the indications are that the nemas infesting the composites are specialized physiological races not capable of infesting others of the known economic host plants. There are indications of gradual adaptation to new host plants, however. Further investigations are being made in this connection.

SUMMARY

(1) The leaf and stem infesting nematode, Tylenchus dipsaci Kühn, has been found to be abundant on the false dandelion, Hypochaeris radicata, along the Pacific coast, from Tacoma, Wash., to San Francisco, Calif. It occurs as well in the true dandelion, Taraxacum officinale, in Western New York, the Province of Ontario, Canada, and at Boston, Mass. According to the literature, it occurs abundantly on these and other composites in Europe.

(2) In addition to producing swellings and distortions of the leaves, the nemas penetrate the developing flower head and produce more or less distortion in that region. Furthermore, in the case of the false and true dandelion they were observed to have actually penetrated into the interior of the seed.

(3) This accounts definitely for their wide distribution on these hosts, for the wind carries the nematode-infested equally well with the nematode-free seed.

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LITERATURE CITED


(9) MASSALONGO, C. 1915. APPUNTI DI ZOOCÉCIDOLOGIA ITALICA. Marcellia 14: 3–10, illus.


(20) Trotter, A. 1905. NUOVE OSSERVAZIONI SU ELMINTOCECIDII ITALIANI. Marcellia 4: 52–54.
A.—Stems of false dandelion, *Hypochaeris radicata*, showing galls produced by the insect *Aulax hypochaeridis* Kieff. These are shown to distinguish them from the galls caused by the stem nematode, *Tylenchus dipsaci*.

B.—Immature flower heads of false dandelion showing stem nematode swellings at the base of the flower head.

C.—Normal flower heads of *H. radicata*; compare with B.

D.—Sections through nematode-infested heads of *H. radicata*. Note the discolored receptacle, which contains hundreds of nematodes.
Dissemination of Tylenchus dipsaci in Seeds

Plate 1-3

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PLATE 2

A.—Photograph of immature seed of *Hypochaeris radicata*, showing nemas coiled inside the seed; taken by transmitted light.

B.—Apical end of a mature seed, showing nematodes within the seed.

C.—Small seedling of *Hypochaeris radicata* showing typical *Tylenchus* swelling in the midrib of the first permanent leaf. This is one of several such plants that resulted from planting seed from a mature infested flower head into a flat of sterilized soil in the greenhouse.

D.—Three typical seed of *Hypochaeris radicata*, taken from an infested flower head. About half the seed from this same lot contained living nematodes.
A.—A flower head of true dandelion, *Taraxacum officinale*, broken open longitudinally to show the slightly discolored receptacle and seed bases. More than 50 per cent of these seeds contained living *Tylenchus dipsaci*.

B.—A single seed of *T. officinale*, from which two living Tylenchi were dissected. Note the seed proper, which was intact, and the normal pappus.

C.—A young plant of *Taraxacum officinale* with three leaves showing typical *Tylenchus* deformities.

D.—A dandelion plant sectioned longitudinally through the crown to show the developing flower heads. Note that when very small they are in the very heart of the plant, protected from ordinary mechanical injury, unquestionably, but ideally situated for infection by the stem nematode.