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Docking Disorder and Root Ectoparasitic Nematodes of Sugar Beet

A. G. WHITEHEAD, R. A. DUNNING and D. A. COOKE

Docking disorder takes its name from the parish in N.W. Norfolk where patches of stunted sugar beet were first reported in 1948 (Hull, 1949), although it almost certainly occurred earlier there and elsewhere on light sandy soils. Typically, affected seedlings grow slowly, soon show signs of nutritional deficiencies, especially of magnesium and nitrogen, and the rootlets are discoloured and misshapen. The condition recurs in the same fields and the same areas in fields, but its severity differs greatly from year to year. Other crops, such as barley, often grow poorly where sugar beet was previously affected.

Anything that damages the roots can, of course, slow the growth of plants and lead to nutritional deficiencies. Hence, it is not surprising that the early work on Docking disorder, done in different places, led to seemingly contradictory conclusions or that the role of ectoparasitic nematodes as a prime cause took long to establish, even though the beneficial effects of treating soils with 'D-D' fumigant were early shown (Shotton, 1958).

The name 'Docking disease' (Gates, 1954) was changed to 'Docking disorder' when Gates (1955) concluded that fungi (*Pythium*, *Fusarium* and *Rhizoctonia*), which were prevalent in the damaged roots of affected sugar beet plants, were not the cause, and suspected a toxin, but Skinner (1956) found no evidence for this. *Fusarium oxysporum* and *Pythium* sp. damaged roots of sugar beet growing in pots, but not enough to account for the effects in the field (Buxton, 1957). Drenching the rows with fungicide at the time of sowing sugar beet improved root shape (Gates, 1955) but possibly not by killing fungi. The organic manure 'shoddy' (wool waste) greatly increased the vigour and yield of sugar beet where Docking disorder occurred, but farmyard manure and inorganic nitrogen gave less consistent improvement (Shotton, 1958; Hull, 1960).

Christie and Perry (1951) described stubby root nematode (*Trichodorus* sp.) damage in the U.S.A. Gough and Welford (1954) suspected these nematodes might be involved but failed to correlate their abundance with Docking disorder, probably because methods of extracting ectoparasitic nematodes from the soil were less good then than now. Gibbs (1959) isolated fungi and nematodes from affected roots but these did not differ in type or number from those isolated from unaffected roots. Also, affected beet taken from the field recovered when replanted in compost whereas beet grew poorly in pots containing the field soil even after it was autoclaved. He suggested the poor growth depended on an unusual chemical or physical condition in the soil; this may have been so, as the soil he used came from the edges of marl pits or from slopes, contained very little clay or organic matter, and slaked completely when moistened.

The soil-borne viruses tobacco rattle (TRV) and the Scottish form of tomato black ring (TBRV-S) were first isolated from sugar beet growing in eastern Scotland (Harrison, 1957; Cadman & Harrison, 1959), but seemed not responsible for the poor growth. TRV is transmitted by stubby root nematodes—*Trichodorus pachydermus* Seinhorst in the Netherlands (Sol & Seinhorst, 1961) and *T. primitivus* Seinhorst in Britain (Harrison, 1961; Mowat & Taylor, 1962). TBRV is transmitted by needle nematodes—*Longidorus elongatus* (de Man) in Scotland (Harrison, Mowat & Taylor, 1961) and *L. attenuatus* Hooper in England (Harrison, 1964). The knowledge that these viruses occur in some

plants in areas where sugar beet grows poorly in East Anglia, but that most of the stunted plants are not infected (Gibbs & Harrison, 1964; Heathcote, 1965), and the report that *Trichodorus* damaged sugar beet in the Netherlands (Kuiper & Loof, 1962), led to a reassessment of the relationship between nematodes and Docking disorder.

Types and symptoms of Docking disorder

Gibbs and Harrison (1963) separated Docking disorder into three 'types': (i) diffuse patches of poorly growing plants with needle nematodes (*Longidorus*) present; (ii) 'kite'shaped patches; (iii) edges of disused marl pits. Whitehead (1965) added two 'types': (iv) areas of excessive drainage; (v) cultivation effects and Whitehead, Greet and Fraser (1966) added another: (vi) diffuse patches of poor growth with *Trichodorus* present. We now restrict the name to one condition, patches of stunted plants caused primarily by *Longidorus* and/or *Trichodorus* feeding on the seedling roots (i.e. (i) and (vi) above). Stunting of beet for other reasons, such as when growing at 'edges of disused marl pits', in 'areas of excessive drainage' or when suffering from 'cultivation effects' should be so described. The reason for stunted plants in the 'kite'-shaped patches recognised by Gibbs and Harrison (1963), Gibbs (1966) and Macfarlane (1966, 1967) is unknown, and the condition was renamed 'Barney patch' from its first recognition at Barney, Norfolk (Dunning & Cooke, 1967).

The plant and field symptoms of Docking disorder are fairly characteristic (Dunning & Cooke, 1967; Jones & Dunning, 1969). Patches of affected plants are ill-defined but coincide roughly with the areas of lightest soil; within the patches most sugar beet plants are very small ('chicks') but some are larger and a few ('hens') may be as large as healthy plants outside the patches. The large and small plants are usually randomly intermingled except where cultivation effects, especially tractor 'wheelings', produce lines of large plants. The leaves of small plants often show signs of magnesium and, especially, nitrogen deficiency.

Where *Trichodorus* spp. predominate, the seedling tap root is often badly injured and may be killed; the laterals then take over its function, leading to a fangy (furcated) storage root. Where *L. attenuatus* predominates, only the laterals are injured, leaving the storage root of normal shape, though small. Hence a fangy root is not characteristic of Docking disorder; conversely anything that kills the tap root (e.g. *Rhizoctonia solani* infection, mechanical damage (Daniels, 1965), acidity, damage by chemicals (Hull, 1960) excessive compaction or waterlogging of the soil) can produce fangy roots. Considerable numbers of *Longidorus* or *Trichodorus* need to be found in the root zone of stunted plants to confirm the poor growth as Docking disorder.

The amount to which a given population of nematodes damages roots depends on their activity, which is much influenced by soil moisture. Damage that could be compensated for when roots are growing vigorously cannot be in soils of poor structure or lacking nutrients, or when plants are harmed by herbicides.

Incidence of Docking disorder

Before 1958 Docking disorder was rarely reported outside West Norfolk and was sometimes confused with toxicity from γ BHC seed dressing; the N.A.A.S. and British Sugar Corporation recorded that it was most prevalent in 1948, 1949, 1954 and, especially, 1953, but was not reported in 1950, 1956 and 1957. In 1958 it occurred more extensively (Gibbs, 1959) but in the early 1960s damage by herbicides sometimes made identification 220

difficult. Since 1963, fieldmen of the British Sugar Corporation have estimated with increasing accuracy the acreage affected (Table 1).

TABLE 1

Docking disorder in England, 1963-70

Estimated loss of root yield (tons) ²
21600
2300
50000
600

¹ Based on monthly pest damage reports from each fieldman of the British Sugar Corporation: 1963-66, acreages severely to moderately affected; 1967-70, total acreages of severely, moderately and slightly affected at the end of June.

² Assuming losses of 6 tons roots/acre (severely affected), 3 tons/acre (moderately affected) and 1 ton/ acre (slightly affected).

Badly affected crops are occasionally ploughed in and the land sown with another crop, but root ectoparasitic nematodes alone rarely kill the seedlings. Since records became more accurate the acreages reported affected have varied greatly in different factory areas and different years (Table 2).

Acreage estin	iated affect	ted by Do	cking diso	rder in six	sugar fac	ctory areas	
	1964	1965	1966	1967	1968	1969	1970
East Anglia							
King's Lynn	255	111	40	1600	200	4240	0
Wissington	153	62	10	188	50	1015	5
Bury St. Edmunds	515	592	2	789	194	1832	20
Cantley	45	5	15	96	0	710	15
Yorkshire							
York*	8	6	1201 -	1451	170	2280	0
Selby*	9	28	16	1200	321	1750	470
	985	804	1284	5324	935	11827	510

TABLE 2

* Much stunting not recognised as Docking disorder before 1966

Although only recently recognised in Yorkshire, we think Docking disorder caused by Trichodorus spp. was prevalent there earlier, because in 1965 we found several infested fields, two of which had more than 8000 T. anemones/litre of soil in the root zone of stunted plants during autumn. Docking disorder has now been reported from most areas where beet is grown on sandy soil, and it seems more prevalent than formerly. Partly, this reflects increasing recognition, but in 1967 and 1969 symptoms were severe. In 1969 it was reported from 14 of the 18 sugar factory areas and eight had more than 1000 acres affected (Bury St. Edmunds, Ipswich, King's Lynn, Newark, Nottingham, Selby, Wissington and York). It can occur after almost any field crop, including grass or after a year's fallow; it is rare after lucerne (Hull, 1960), and is commonest after barley because barley usually precedes beet in the rotation.

Methods of growing sugar beet have changed greatly since Docking disorder was first noted and these changes may have contributed to its apparent increase. Sugar beet seedlings are now exposed longer to the attacks of nematodes because of early sowing, and to more nematodes per seedling, because of wider spacing and the use of rubbed and graded or monogerm seed, instead of natural (multigerm) seed. Pre-emergence herbicides not only kill weeds on which the nematodes might otherwise feed but can also slow the growth of beet seedlings (Hull, 1966) and may make them suffer more from nematode damage. Damage may be enhanced by the depletion of organic matter, resulting from the replacement of livestock and leys by cereals, and from straw burning and deep ploughing (Hull, 1960).

The nematodes

Species and damage. Kuiper and Loof (1962) associated *T. teres* Hooper (syn. *T. flevensis* Kuiper and Loof) with stunting, fangy roots and yield loss in sugar beet on new polder soil in the Netherlands. Evidence that *L. attenuatus*, *L. elongatus*, and *Trichodorus* spp. damage sugar beet and other field crops in England was obtained: (i) by showing that these nematodes caused specific types of root damage on sugar beet seedlings growing in pots containing steamed soil inoculated with the nematodes; (ii) by relating the abundance of nematodes around the roots during spring and early summer with root symptoms and stunting of field plants (Table 3) (Whitehead, 1965, 1966, 1969; Whitehead & Hooper, 1970).

TABLE 3

Average numbers of Longidorus or Trichodorus in the soil close to sugar beet plants of different sizes growing in parts of fields affected by Docking disorder

Number of fields examined	Close to stunted plants	Close to larger plants
	L. attenuatus	/litre of soil
25*	143	70
	L. elongatus	litre of soil
3	335	104
	Trichodorus sp	p./litre of soil
24	2200	800

* In ten of these fields there were on average only 31 L. attenuatus/litre in the soil close to large plants in parts of fields unaffected by Docking disorder.

Longidorus spp. (needle nematodes) are among the largest plant-parasitic nematodes; many adults exceed 5 mm long and to the naked eye are visible adhering to plant roots. *Trichodorus* spp. (stubby root nematodes) are smaller, the adults usually shorter than 1 mm and invisible to the naked eye. Both *Longidorus* and *Trichodorus* feed on root tips.

Longidorus spp. have long feeding stylets that are probably inserted deeply into roots; presumably in response to saliva injected, the root tip swells and later may show a necrotic spot, probably where the stylet was inserted. Sections of root tips galled by *L. attenuatus* show a row of necrotic cortical cells, extending deep into the root tip, marking the probable region of stylet penetration. *L. elongatus* can stop the tap roots of beet seedlings growing, whereas *L. attenuatus* usually harms only the lateral roots. Both cause galls on sugar-beet roots. *L. elongatus* also damages strawberries (Sharma, 1965; Seinhorst, 1966), 222.

grass, carrots, kale and probably many other crop plants (Whitehead, 1969; Whitehead & Hooper, 1970).

Trichodorus spp. have shorter stylets that penetrate less deeply than those of Longidorus spp. Their feeding often stops tap roots growing. The terminal and lateral root tips become stubby (i.e. stunted and slightly swollen), turn brown or black and laterals may be zig-zagged. When the tap root stops growing or is killed, lateral roots near the soil surface thicken and replace it. When Trichodorus are abundant, the downward-growing laterals also are injured and laterals grow only near the soil surface, where conditions are less favourable for the nematodes. Although a shallow root system is a common result of Trichodorus injury, effects differ because of the influence of secondary pathogens or soil conditions. Saliva injected by feeding nematodes seems to cause only local damage, and the leaves show symptoms because the damaged roots do not supply them with enough nutrients.

When sugar beet seedlings injured by *Longidorus* or *Trichodorus* are washed free from soil containing the nematodes many injured roots resume growth and new rootlets form close to those which were killed. Hence, in the field, plants may recover when the nematodes stop feeding on the roots, as during a dry spell (Whitehead & Hooper, 1970).

Other plant-parasitic nematodes are common in fields where Docking disorder occurs and may add to the damage caused by *Trichodorus* and *Longidorus*. *Pratylenchus* spp. and *Tylenchorhynchus* spp. multiply greatly on barley, which usually precedes sugar beet on light, sandy soils. *P. minyus* Sher and Allen occurs sporadically in the roots of stunted sugar beet and may feed ectoparasitically on the roots. *Tylenchorhynchus dubius* Bütschlii does not cause obvious lesions on sugar beet roots and seems to feed mostly on root hairs (Whitehead & Hooper, 1970). *Hemicycliophora similis* Thorne were found attached by their stylets to swollen root tips of sugar beet seedlings in the Docking area of Norfolk (Whitehead, 1967).

Soil sampling and extraction. To relate the abundance of ectoparasitic nematodes to injury, crops must be sampled at the correct time, because fewer occur in soil taken near the roots of small seedlings as the season advances and more near the roots of larger plants, which provide more feeding sites. The abundance of ectoparasitic nematodes was related to injury by taking soil samples from mid-May onwards in the rows close to large and small seedlings, and at 2-inch (5 cm) intervals away from the plants at right angles to the crop rows. The numbers on the roots are related to the damage and some estimate of these was obtained by lifting seedlings carefully, washing their roots in water and counting the nematodes in the water and still attached to the roots. The seedlings, their roots and the adhering soil, were weighed and the number of nematodes per gram calculated. Some species, e.g. H. similis and L. elongatus, remain firmly attached to sugar beet roots when taken from soil, and L. attenuatus sometimes remain close to the roots on which they have been feeding, by coiling or by getting entangled in root hairs or fungal hyphae. Trichodorus is easily dislodged because it is short, does not coil and its stylet does not penetrate deeply. Later in the season, when the root systems are larger and the soil usually drier, many roots are broken and so many nematodes are dislodged when plants are lifted that the method cannot estimate the number feeding on the roots.

It is almost impossible to estimate total populations of ectoparasitic nematodes in soil. Eggs are laid singly, must be extracted by centrifugal flotation (Flegg & McNamara, 1968) and can be identified only when they have a characteristic shape, as those of *Longidorus* spp., and only when one species of each genus is present, which is rare.

Identifying the larvae, either within eggs or soon after hatching, is difficult. Also, even the best methods rarely extract more than three-quarters of all stages. Nevertheless, suitable methods extract larvae and adults consistently and are adequate to compare numbers around healthy and diseased plants, to follow changes with time or depth, and to assess the effects of such control measures as the use of nematicides.

Small ectoparasites, such as *Tylenchorhynchus* spp., *Tylenchus* spp. and *Paratylenchus* spp., were best extracted by a Baermann method (Whitehead & Hemming, 1965) but this was unsuitable for *Trichodorus* and *Longidorus*. *L. attenuatus* and *L. elongatus* from sandy soils and *L. elongatus* from peat soil were extracted satisfactorily by decanting a suspension of soil in water onto a sieve with 100 μ apertures submerged under a constant head of water. The two-flask method (Seinhorst, 1955) extracted *Trichodorus* spp. satisfactorily from sandy soils (Whitehead & Hooper, 1970).

Geographical and depth distribution. Seven species of stubby root nematodes (Trichodorus anemones Loof, T. cylindricus Hooper, T. pachydermus Seinhorst, T. primitivus Seinhorst, T. similis Seinhorst, T. teres Hooper and T. viruliferus Hooper) and four species of needle nematodes (Longidorus attenuatus, L. elongatus and occasionally L. caespiticola Hooper and L. leptocephalus Hooper) occur in fields where beet suffer from Docking disorder. Two or more of these species often occur together in the same field. Five species of Trichodorus have been found in one field.

The commonest species of *Trichodorus* in sandy soils prone to produce Docking disorder are *T. pachydermus* and *T. primitivus*, but *T. cylindricus* and *T. teres* are abundant in some places. *L. attenuatus*, the commonest needle nematode in such soils in eastern England, also occurs in the Midlands in sandy soils but is uncommon in the low-lying sandy soils of the Vale of York, where *Trichodorus* is abundant. *L. elongatus* is abundant in some Fen peat soils and in sandy soils in the West Midlands, but is rare in the drier sandy soils of eastern England (Whitehead & Hooper, 1970).

The girth of *Trichodorus* spp. and *Longidorus* spp. restricts them to major soil passages. The surface 2 inches (5 cm) of light, sandy soils where *L. attenuatus* and *Trichodorus* spp. stunt sugar beet may contain few nematodes during late spring or early summer, when the soil is drying, but there may be many 2-8 inches (5-20 cm) deep (Cooke & Draycott, 1970). *T. teres* was most abundant 5-10 cm deep in polder soil (Kuiper & Loof, 1962) and *T. cylindricus* more abundant above plough depth than below it; by contrast *L. attenuatus* was often more abundant below plough depth (Whitehead & Hooper, 1970). Drying of the top soil early during the growing season can prevent the nematodes from moving and feeding, whereas deeper down they can still be active.

Bionomics. Species of *Trichodorus* and *Longidorus* can feed on the roots of many plants but seem to multiply to different extents under the same crops in different seasons and in different places (Taylor, 1967; Whitehead, 1967; Cooke & Hull, 1967; Whitehead & Hooper, 1970; Whitehead, Fraser & Greet, 1970). They can survive a long time without food so they are not greatly affected by bare fallowing (Harrison & Hooper, 1963; Whitehead & Hooper, 1970).

L. elongatus, L. attenuatus and T. teres are parthenogenetic, but other Trichodorus spp. have functional males. There are four larval stages and development from egg to adult ranges from a few months to a year or more. They also multiply slowly, so the populations are diminished for a long time after the soil is fumigated (Whitehead & Tite, 1968; Cooke, Draycott & Hull, 1969; Whitehead, Fraser & Greet, 1970).

The use of herbicides and 'drilling to-a-stand' means there are fewer roots than 224

previously for the nematodes to feed on when the beet are in the seedling stage and most vulnerable. Over what distance sugar beet roots attract nematodes is unknown, but T. viruliferus were attracted to roots of apple from at least 8 cm (Pitcher, 1967). That L. elongatus are attracted by roots of beet and other plants in Fen peat soils was shown by the extent to which they were aggregated around root tips (Whitehead & Hooper, 1970). Also, L. attenuatus were more abundant around the roots of both seedling and mature beet when widely spaced than when at close spacing (Table 4) (Cooke, 1968).

TABLE 4

Number of Longidorus in soil close to sugar beet plants at different spacings, Herringswell, W. Suffolk, 1967

Samples on 30 May		Samples on 20 October	
Seedling spacing (inches)	Longidorus/litre soil	Plant spacing (inches)	Longidorus/litre soil
6.1	296	14.2	55
2.5	286	11.2	67
1.4	198	10.4	34
0.4	180	9.5	31

Soil conditions will affect the ease with which the nematodes can move to root tips; they do so more readily in light than heavy soils and in moist than in dry soils. Seedlings have fewer roots than older plant and are less able to withstand attack. Hence, with a given population of nematodes damage is greatest in sandy soils that are weed free, drilled to a stand and are wet when the seedlings are small.

Factors affecting yield loss

Although sugar beet seedlings whose roots are damaged by *Trichodorus* or *Longidorus* are usually smaller than those that are not, there is no close relationship between nematode numbers and yield losses in different fields and years. The importance of root damage depends less on the species and abundance of the nematodes than on the time when the roots are attacked and the vigour of the seedlings, both of which are influenced by type, structure, moisture and nutrient content of the soil.

Soil. Pizer (1954) stated that there was little organic matter in the soils of affected fields, Gates (1954) found Docking disorder worst in areas of light soil with least organic matter and Gibbs (1959) recorded that it occurred in the same patches every year. Brenchley (1968), who photographed affected patches from the air, found that the disorder was often associated with changes in soil structure and texture and almost entirely confined to drift soils. Severe effects were frequently associated with areas of poor soil structure, seemingly the result of solifluxion or cryoturbation in periglacial conditions, and he thought the poor structured areas provided a favourable environment for the nematodes as well as being sometimes directly responsible for poor growth. Similar, irregular, diffuse patches of stunted beet occur on the soils derived from Bunter sandstones in Nottinghamshire and the West Midlands, and on the wind-deposited sands of Lincolnshire and Yorkshire. Table 5 gives analyses of soils from some fields where nematode infestations have caused stunting and where some of our trials have been made.

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TABLE 5

Mechanical analysis, organic matter content and pH of soil from parts of fields with Docking disorder

Site	Coarse sand (2000– 200 µ) %	Fine sand (200–20 μ) %	Silt (20–2 µ)	Clay (<2 μ)	Organic matter %	pH (1 g soil in 2 · 5 ml water)
Docking, Norfolk	67	24	3	6	0.7	7.2
Gayton, Norfolk	60	27	3	9	1.2	8.2
Stoke Ferry, Norfolk	24	18	14	44	43	5.3
Herringswell, W. Suffolk	31	60	2	6	0.9	7.7
Thornton, E. Yorkshire	57	33	3	5	1.8	7.5

Soil from the worst affected patches usually contains less than 10% of clay and more than 80% of coarse fractions (fine and coarse sand). Nematodes also occur in better soils but here they are less damaging: for example, in the peat soils of Methwold Fen, near Stoke Ferry, Norfolk, *L. elongatus* is abundant and stunted sugar beet seedlings in 1969 (Whitehead & Hooper, 1970), producing typical Docking disorder symptoms, but the crop recovered and yielded satisfactorily.

Jones, Larbey and Parrott (1969) suggested that the abundance and activity of nematodes in a soil depended on their dimensions in relation to the cross section and configuration of soil spaces. Whereas root endoparasites such as *Heterodera*, which soon become sedentary inside the roots, can be plentiful in both fine and coarse soil, *Longidorus* and *Trichodorus* are abundant only in coarse soils. When prepared as seed-beds these soils provide a favourable environment for *Longidorus* and *Trichodorus* and, if the soil is excessively loose, beet can be severely damaged; sugar beet seedlings often grow better in tractor 'wheelings' than elsewhere, possibly because the nematodes move less readily through partly compacted soil. However, the effects of compaction are complex, and severe compaction or slaking of these soils can be damaging by physically restricting root growth or by making the soil nearly anaerobic. Heavier sandy soils that are compacted, perhaps by untimely cultivation, sometimes produce shallow, fangy roots and stunted, nutrient-deficient tops reminiscent of Docking disorder.

Marl applied to Norfolk light land during the 17th, 18th and 19th centuries (Fussell, 1959; Prince, 1964) has now leached from the top soil. Marling makes the soil more stable, helps root growth and decreases wind erosion; it has been done recently in sandy fields in E. Yorkshire (Park, Brown & Wright, 1970).

Rainfall. Hull (1960) observed that Docking disorder is most severe after wet springs, and Jones *et al.* correlated April–June rainfall with the acreage of beet stunted in the Cantley, Bury St. Edmunds, King's Lynn and Wissington sugar factory areas. They ranked the severity of Docking disorder at the end of June as 1967 (most), 1964, 1965, 1968, 1966 (least); 1967 was exceptionally wet in April–June and 1966 was drier than average. This ranking accorded well with the weekly cumulative rainfall during the last three weeks of May; the ranks accorded poorly with rainfall earlier and with rainfall later the accord was lost. Rainfall is the main factor affecting moisture tension in coarse, free-draining soils. The moisture tension favouring nematode movement is in the range 0·1–0·25 atm., i.e., 100–250 cm water (Wallace, 1963). Jones *et al.* suggested that the summation of ectoparasitic nematode activity during spring was proportional to cumulative rainfall, and that May rainfall determined the severity of stunting; rainfall had less 226

influence after dry spells in May or early June because such spells prevent nematodes from moving and feeding and allow plant roots to extend undamaged.

In 1969 a greater area was reported affected by Docking disorder than ever before, in the factory areas considered by Jones *et al.* three times that reported in 1967; rainfall for May 1969 was slightly less than in 1967, but June was wetter. In the same areas in 1970 only 40 acres were estimated to be affected (Table 2); May and June were exceptionally dry. Frequent rain not only increases nematode activity but also leaches nitrogen from the root zone (Draycott & Last, 1971) leaches herbicides from the soil surface into the root zone and slakes and compacts the soil. These other effects alone do not produce Docking disorder, but often add to the damage done by nematodes.

Nutrients. Soils prone to producing Docking disorder contain little available mineral nitrogen, usually only about 0.05 ppm or even less (P. J. Last, *personal communication*) and little magnesium (Pizer, 1954). Nitrogen leaches readily from soils with little clay and loss is greatest during wet springs, which also favour nematode activity and root damage. The seedlings cannot then get enough nutrients from the surface soil and consequently show the signs of nitrogen and magnesium deficiency characteristic of Docking disorder.

Control of Docking disorder

Killing the nematodes in the soil is the only reliable way of preventing Docking disorder, but the damage can be ameliorated in various ways, some of which are:

A. Minimise the effects of nematode feeding.

- (i) Avoid practices that might weaken plant growth, such as
 - (a) sowing too deep or too early,
 - (b) applying too much herbicide,
 - (c) harming soil structure.

(ii) Adopt all practices that encourage plant growth, such as

- (a) controlling damage from other pests or diseases and from soil blowing,
 - (b) applying organic matter,
 - (c) applying extra nitrogen.

B. Minimise the amount of nematode feeding.

- (i) Provide alternative or additional feeding area, by
 - (a) inter-row cropping,
 - (b) sowing sugar beet seeds closer together.
- (ii) Limiting nematode movement, by
 - (a) marl, which also has soil-stabilising and some nutrient benefits,
 - (b) a firm seedbed.
- (iii) Kill the nematodes or repel them from the roots.

Evidence of the value of some of these practices has been reviewed above, and that for the use of additional nutrients or nematicides is given below.

Nutrients. Much of the yield loss from Docking disorder is because damaged roots do not absorb enough nutrients, and some of this loss can be partly compensated for by giving extra nitrogen to the seedbed or as a top dressing. Large dressings of seedbed

nitrogen sometimes enable seedlings to recover from early nematode attack and produce roots of better shape and larger yield.

In several field trials from 1948 to 1954 magnesium applied as kieserite at 4-5 cwt/acre did not improve growth, whereas nitrogen in various forms often did (Shotton, 1958). In one trial, plots given 8 cwt 'shoddy' (wool waste) plus 2 cwt 'Nitrochalk'/acre yielded 12 tons roots/acre whereas those given the equivalent amount of nitrogen as sulphate of ammonia (4 cwt/acre) yielded only 5 tons/acre. In the same field in 1956, when stunting was again severe, root yield was increased from 3 tons/acre with inorganic fertiliser only, to around 10 tons/acre with 'hoof and horn' or 'shoddy' (amounts used not specified) (Shotton, 1958); presumably the benefit arose from the slow release of nitrogen from the organic fertilisers.

Of several granular fertilisers placed in the root zone of severely stunted plants in June 1965 only nitrogen increased yields (Dunning, Heathcote, Winder & Tinker, 1966), and solutions of nitrogen sometimes improved yields when similarly placed (Dunning & Winder, 1969b). In a trial at Thornton, Yorkshire, where all beet were given 1.2 cwt/ nitrogen/acre in the seedbed, an extra 1 cwt of nitrogen/acre added to the seedbed increased sugar yield from 12.7 to 23.9* cwt/acre and improved root shape; when applied as a top dressing it increased yield similarly without improving root shape (Dunning & Winder, 1967).

The effect of 0, 0.66, 1.32 and 1.98 cwt nitrogen/acre applied in the seedbed as 'Nitrochalk' was tested at 15 sites between 1967 and 1969 (Draycott & Cooke, 1968, 1969; Cooke & Draycott, 1970).

In 1967 at Messingham, Lincolnshire, where Trichodorus was abundant, roots were badly damaged and yield was small, the largest dressing of nitrogen most improved root shape and sugar yield; at Herringswell, Suffolk, on a similar soil in the same year, where nematodes were few, root systems were normal and yield was average, the three amounts of nitrogen gave equal yield increases (Table 6). In no trial did top dressing with 0.66 cwt nitrogen/acre in June improve root shape; on average the best root shape and sugar yield were from plots given 1.98 cwt nitrogen/acre in the seedbed, which is almost twice the nationally recommended amount. In four of the 15 trials, nitrogen applied in a slow release form, as isobutyridene diurea, gave better yields than the equivalent amount as 'Nitrochalk'.

TABLE 6

Effect of nitrogen applied to the seedbed on root fanginess and sugar yield at sites with and without Docking disorder, 1967

	Messingh	am, Lincs ¹	Herringswell	, W. Suffolk ²
Nitrogen	Root	Sugar	Root	Sugar
applied	fanginess	yield	fanginess	yield
cwt/acre	(0-5)†	(cwt/acre)	(0-5)†	(cwt/acre)
0	2·4	33·5	0.5	43.9
0.66	2·3	38·6	0.5	64.8***
1.32	2·1	48·3**	0.4	65.8***
1.98	1·7**	53·8***	0.5	63.5***

¹ Trichodorus spp. (mainly T. primitivus and T. pachydermus), 1750/litre of soil in April: crop affected by Docking disorder.

² Longidorus attenuatus, 10/litre of soil in April: crop not apparently affected by Docking disorder. $^{+}0-5$ = scale of increasing root fanginess. *, **, *** Statistically significant root shape improvement, or yield increases, at 5%, 1% and 0.1%

levels of probability respectively.

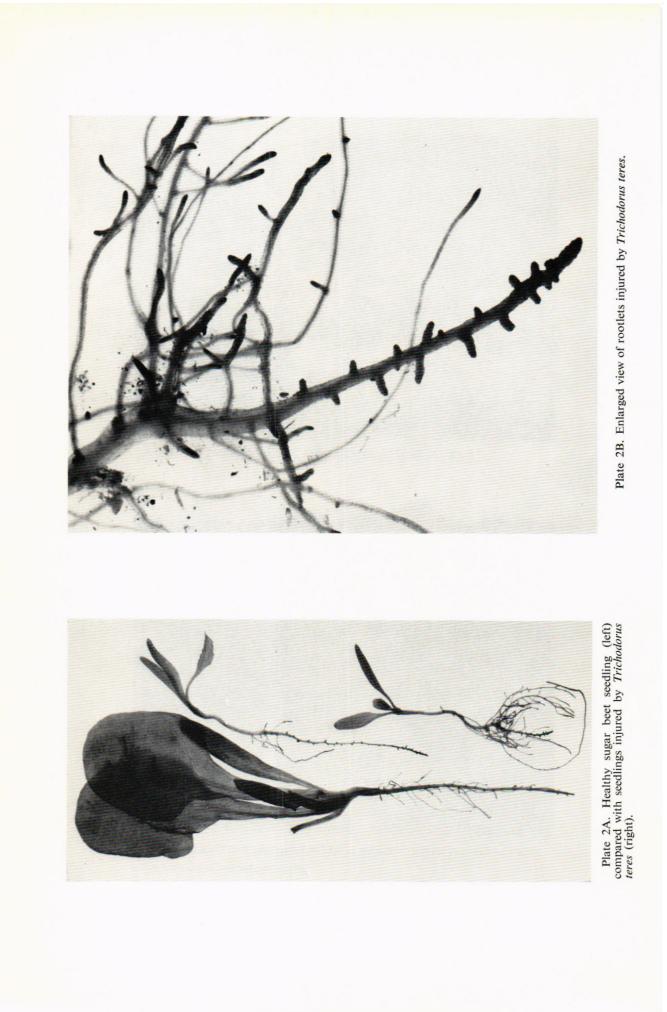


Plate 1A. Field of sugar beet with Docking disorder.



Plate 1B. Effect of tractor wheelings in field of sugar beet with Docking disorder. Photos: Broom's Barn Experimental Station [facing p. 228]

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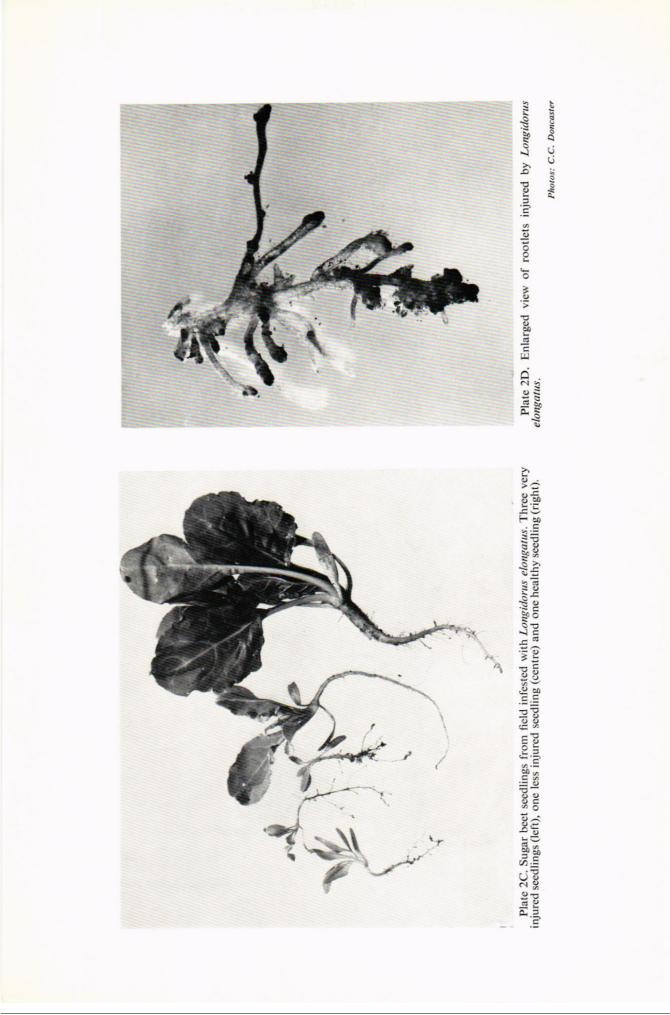




Plate 3A. Plot fumigated with 'D-D' (400 lb/acre) in sugar beet field with Docking disorder.



Plate 3B. Effect of a granular nematicide applied in the seed furrow at sowing (left) compared with an untreated row (right).

Photos: Broom's Barn Experimental Station

The results of these and other experiments (Whitehead, Tite & Fraser, 1970) show that increasing nitrogen fertiliser can increase yield, especially when in slow release form or when the supply is maintained in the surface soil by top dressing, but is not a reliable method of preventing Docking disorder.

Nematicides. Longidorus and Trichodorus feed on many different species of plants and can survive long periods in the soil without host plants, so neither changing crops nor fallowing land will greatly decrease populations, which can be done only with nematicides. Nematicides have been tested on sites prone to Docking disorder since 1955, but only since 1964 has nematode control been measured.

Overall treatment with fumigant nematicides. 'D-D' soil fumigant (1,3 dichloropropene-1,2 dichloropropane mixture) was first tested by Eastern Region, N.A.A.S., at Docking in 1955, where it and ethylene dibromide greatly improved the growth of sugar beet. In two fields, where Docking disorder occurred in 1958, injecting with 'D-D' during autumn 1957 greatly increased yields and gave less fangy roots. At 'Washpit Breck', Docking, also, 'D-D' applied during the autumn of 1955 increased the yield of sugar beet grown in 1958 from 4 to 13 tons/acre and decreased the percentage of fangy roots from 85 to 26 (Shotton, 1958). 'D-D' was not tested again until Docking disorder was attributed to ectoparasitic nematodes (Whitehead & Cooke, 1965).

Heathcote, Greet and Whitehead (1966) showed that, in 1964 in two fields prone to Docking disorder, 33.5 gal 'D-D' or chloropicrin/acre injected into the soil in December 1963 killed many nematodes, including *L. attenuatus*, and greatly increased the yield of sugar beet. 'D-D' or chloropicrin point-injected 6 inches deep at 12-inch centres (33.5 gal/acre) into sandy soil in February 1965 killed more than 95% of the *L. attenuatus* down to 20 inches. *Trichodorus* are also killed by large doses of 'D-D'. At Gayton and Santon Downham in Norfolk, fumigating the soil in this way early in 1965 with 'D-D' or chloropicrin gave good crops of sugar beet taken in 1965, 1966 and 1967 (Table 7) (Whitehead, Fraser & Greet, 1970).

TABLE 7

Effect of fumigating soil during winter 1965 on yield of sugar (cwt/acre)

	Gay	ton, No	rfolk	Santon D Nor	
Fumigation treatment	1965	1966	1967	1965	1966
Untreated 'D-D', 33.5 gal/acre at 12-inch centres	47.9	52.3	36.9	39.3	56.6
overall	65.7***	60.9	52.4***	56.7*	74.3***
Chloropicrin, 33.5 gal/acre at 12-inch centres overall	67.8***	57.2	49.9***	64.0**	62.3

*, **, *** Statistically significant yield increases at 5%, 1% and 0.1% levels of probability respectively.

At Thornton, Yorkshire, where untreated soil had 6000 *T. anemones*/litre in April 1967, 17 gal 'D-D'/acre injected 6 inches deep at points 12 inches apart during January 1967 increased sugar yield from 27 to 53*** cwt/acre (Dunning & Winder, 1968). As little as 10 gal 'D-D', 'Telone' (mostly 1,3 dichloropropene) or ethylene dibromide/acre trickled onto the furrow bottom while ploughing during early autumn, killed 75% or more of

Trichodorus and *Longidorus*. In one trial, 11 gal 'D-D'/acre increased sugar yield from 24.3 to 40.9* cwt/acre. Table 8 gives the results of other trials, in one of which 6 gal 'D-D'/acre increased sugar yield as much as did 24 gal/acre.

Applying soil fumigants deeper than 6 inches on the furrow bottom during late autumn or winter was much less effective, probably because the fumigants penetrated the deeper (warmer) layers of the soil rather than the surface (colder) layers; treating very wet soils was also ineffective (Whitehead & Tite, 1968; Whitehead, Tite & Fraser, 1970).

TABLE 8

Effect of small doses of fumigant applied to the furrow bottom during ploughing in autumn or winter on sugar yield of beet crops sown the next spring

Site	Fumigation treatment	Sugar yield (cwt/acre)
Docking, Norfolk	Untreated Ethylene dibromide, 10 gal/acre	29·3 42·0**
	Untreated 'D-D', 10 gal/acre 'D-D', 20 gal/acre	23·3 31·9* 35·0**
Gayton Thorpe, Norfolk	Untreated 'D-D', o gal/acre 'D-D', 12 gal/acre 'D-D', 24 gal/acre	44·4 53·1** 55·0** 52·3**

*, **, Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

'D-D', 'Telone', ethylene dibromide, chloropicrin and other soil fumigants inhibit the bacteria that convert ammonium to nitrate, and thus retard the nitrification of ammonium nitrogen formed by mineralisation of soil organic nitrogen or added as fertiliser. Fumigation can also cause a flush of mineralisation of soil organic nitrogen (Gasser & Peachey, 1964). Hence, after fumigation, more of the mineral nitrogen in the soil is in the ammonium form, which is adsorbed onto the clay particles and humus, and less is in the more readily leached nitrate form. Also the total amount of mineral nitrogen in the soil may be increased.

At Herringswell, Suffolk, 33.5 gal 'D-D'/acre injected at points 12 inches apart during December 1965, slowed nitrification and thus decreased leaching, but did not increase the total amount of mineral nitrogen in the soil profile down to 24 inches next May. Ninetyseven per cent of the plant parasitic nematodes in the soil were killed, and the yields of sugar beet, barley, ryegrass and potatoes were greatly increased. In 1968 unfumigated plots and plots fumigated in 1965 or 1966 contained similar amounts of mineral nitrogen, similarly distributed through the soil profile, but those fumigated in 1967 had more mineral nitrogen, especially in soil down to 4.5 inches. Docking disorder was not apparent in any plot, but all fumigated plots contained few *L. attenuatus* and yielded more sugar than unfumigated plots (Table 9); this suggests that most of the yield increase was from killing nematodes, not from increasing soil nitrogen (Cooke, Draycott & Hull, 1969).

In 15 trials in 1967–69 less nitrogen fertiliser was needed on average to achieve optimum yield after fumigation with 33.5 gal 'D-D'/acre, partly because 'D-D' increased the amount of mineral nitrogen in the surface soil and partly because root systems were not damaged by nematodes and were therefore better able to absorb nutrients (Table 10) (Draycott & Cooke, 1968, 1969; Cooke & Draycott, 1970).

TABLE 9

Mineral nitrogen measured in the soil, numbers of L. attenuatus and sugar yield in 1968 after fumigation treatments in 1965–67 at Herringswell, W. Suffolk

Fumigation treatment		Mineral nitrogen (lb/acre)	L. attenuatus (no./litre soil)	Sugar yield (cwt/acre)
Untreated		126	110.8	65.1
'D-D', 33.5 gal/acre at 12-inch centres overall	in 1965	119	9.8	74.9
'D-D', 33.5 gal/acre at 12-inch centres overall	in 1966	117	4.4	75.4
'D-D', 33.5 gal/acre at 12-inch centres overall	in 1967	162	0.3	76.9

TABLE 10

Mean effects of nitrogen applied to the seed bed and fumigating the soil in winter, on sugar yield at 15 sites, 1967–69

Fumigation treatment	Nitrogen	applied to	o seedbed	(cwt/acre)
	0	0.66	1.32	1.98
		Sugar yiel	d (cwt/acr	e)
Untreated	33.7	41.9	44.8	46.2
'D-D', 33.5 gal/acre at 12-inch centres overall	49.4	58.3	58.2	58.3

Least significant difference between any two treatment means—4.6, 6.1 and 7.9 at 5%, 1% and 0.1% levels of probability respectively.

Row treatment with small amounts of fumigant. As sugar beet is a row crop (row width 21 inches on average) and Docking disorder is principally a seedling problem, our more recent work has concentrated on treating the rows with fumigant or systemic nematicides. This is cheaper than treating the whole field and enables the beet seedlings to develop a good primary root system and to grow vigorously. Once the plants are well established, attack by nematodes from the soil between the rows seems not to be damaging.

'D-D' injected during January 1965, 6 inches deep at points 12 inches apart in all directions, was compared with 'D-D' injected 6 inches deep at points 12 inches apart along the lines of the predetermined sugar beet rows, spaced 21 inches apart. All treatments increased sugar yield in 1965, more from injections of 13.5 or 19 gal/acre along the rows than from 38 gal along the rows or 24 or 33.5 gal injected at points 12 inches

TABLE 11

Yield of sugar and of barley grain at Gayton, Norfolk, in 1965–67 after two methods of fumigation in January 1965

	Yiel	ds (cwt/ac	re)
Fumigation treatment	Sugar 1965	Barley grain 1966	Sugar 1967
Untreated 'D-D', 13.5 gal/acre at 12-inch centres in rows 21 inches apart 'D-D', 19 gal/acre at 12-inch centres in rows 21 inches apart 'D-D', 38 gal/acre at 12-inch centres in rows 21 inches apart 'D-D', 24 gal/acre at 12-inch centres overall 'D-D', 33.5 gal/acre at 12-inch centres overall	$52 \cdot 3 \\ 64 \cdot 2^{***} \\ 61 \cdot 5^{**} \\ 56 \cdot 6 \\ 56 \cdot 2 \\ 57 \cdot 0$	26·9 31·1** 30·4** 30·5** 30·0* 31·0**	39·7 50·9*** 54·2*** 54·1*** 51·4*** 51·4***

*, **, *** Statistically significant yield increases at 5%, 1% and 0.1% levels of probability respectively.

apart, probably because the larger amounts damaged plant growth. The tops and roots were removed from all plots; all fumigation treatments gave similar grain yield increases in barley sown in 1966. Sugar beet was grown in 1967, when again there were large benefits from the 'D-D' applied by either method in 1965 (Table 11) (Whitehead, Tite & Fraser, 1970).

'D-D' applied 10 inches deep on the furrow bottom during ploughing in early November 1966 in rows 18 inches apart and marked at intervals of 12 ft by sowing winter wheat, so that sugar-beet rows could be drilled in the fumigated bands next spring (Whitehead & Tite, 1968), killed few *T. cylindricus* in the top 8 inches of soil but many in the layer 12–20 inches deep. Sugar yield was increased from 23·1 to 42·7** cwt/acre by applying 9 gal 'D-D'/acre in this way, but 4·5 gal had much less effect and 2 gal had none. 'D-D' applied in rows by 'plough-sole' (i.e. as above) or 'knife-coulter' methods in September 1967 increased sugar yields in 1968 (Table 12) (Whitehead & Tite, 1969).

TABLE 12

Yield of sugar at Docking, Norfolk, 1968, after fumigating the rows during September 1967

	Yield of sugar (cwt/acre)			
Fumigation treatment (continuous flow in rows 18 inches apart)	'Plough-sole' application	'Knife-coulter' application		
Untreated	28.9	34.4		
'D-D', 6.5 gal/acre	38.6*	35.9		
'D-D', 13.0 gal/acre	40.8**	41.2*		

*, ** Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

Row fumigation during spring shortly before drilling is an accepted practice in parts of the U.S.A. for some field crops, but the soil in England had been thought to be too cold during March and April for the fumigant to disperse before sugar beet seeds germinate. However, in an experiment at Docking in 1967, 4, 8 and 16 gal 'Telone'/acre trickled 10 inches deep close to sugar beet rows immediately after sowing killed many *T. cylindricus* in the rows and increased sugar yields from 22·1 to respectively 45.9^{***} , 40.4^{**} and 35.1^* cwt sugar/acre. Trials at Docking in 1968 tested different amounts of 'D-D' and 'Telone' injected 3, 6 and 9 inches deep by knife-coulters in the predetermined beet rows three weeks before sowing (Whitehead & Tite, 1969). Yield increases were greatest from the 6-inch and 9-inch treatments, but Table 13 gives results averaged over the three depths.

These experiments showed that as little as 6 gal 'D-D' or 4 gal 'Telone'/acre injected beneath the rows at or before drilling could control *L. attenuatus* and *Trichodorus* spp. well enough to allow the seedlings to grow normally. In 1969, 6 gal 'D-D'/acre, injected by knife-coulters 6–8 inches deep along the rows two weeks before sowing, killed 84% of *T. cylindricus* at one site and 91% of *L. attenuatus* at another in the rows, but only 25% and 68% respectively 5 inches from the rows, and none 10 inches from the rows (Cooke, Dunning & Winder, 1970).

Row fumigation during spring is commercially practical and was successful at Ripper Farms Ltd., Docking, in 1968 and 1969. In rows thus treated with 6.4 gal 'D-D'/acre two to three weeks before sowing in 1968, 85% of *T. cylindricus* were killed, and seedlings growing in the rows in June weighed more than ten times as much as seedlings in untreated 232

TABLE 13

Effect on sugar yield of fumigating the rows three weeks before sowing at Docking, Norfolk, 1968

Fumigation treatment	Sugar yield		
(continuous flow in rows 18 inches apart)	(cwt/acre)		
Untreated	40·2		
'D-D', 4 gal/acre	46·6*		
'D-D', 8 gal/acre	48·2*		
Untreated	39·4		
'Telone', 4 gal/acre	45·8		
'Telone', 8 gal/acre	49·8**		

*, ** Statistically significant yield increases above the respective controls at 5% and 1% levels of probability respectively.

rows; treated rows yielded 18 cwt/acre more sugar than untreated rows (Whitehead & Tite, 1969). Seedlings from rows similarly treated in 1969 with 6.4, 9.6 or 12.8 gal 'D-D'/ acre weighed ten to 20 times more than seedlings from untreated rows; rows treated with 6.4 gal/acre yielded 12 cwt more sugar/acre than untreated rows (Whitehead, Tite & Fraser, 1970). In 1970 some 1000 acres were treated commercially with 'D-D' or 'Telone', mainly in East Anglia.

Row treatment with small amounts of systemic nematicide. At Hopton and Swaffham, Norfolk, in 1964, sugar yield was increased or fanginess of roots was decreased by granules containing dibromochloropropane, phorate or thionazin, applied at 4-22 oz a.i./acre in the seed furrow. These results first indicated that very small amounts of pesticide placed close to sugar beet seeds could lessen losses from Docking disorder (Dunning & Winder, 1969b). In 1966 menazon seed dressing, and in 1967 thionazin and phorate granules in the seed furrow, improved the shape and yield of sugar beet roots in soil infested with T. anemones at Thornton, Yorkshire, but in other fields thionazin and phorate damaged the beet and menazon was ineffective.

Of 29 pesticides tested by applying small amounts in the seed furrow at sowing in 1967, 1968 and 1969, aldicarb ('Temik') controlled Docking disorder best. Small amounts

TABLE 14

Effect of systemic nematicides applied with the seed on root fanginess and sugar yield

Systemic nematicide treatment	Thornton, E. Yorkshire			Hellesdon, Norfolk		
	oz a.i./ acre	Root fanginess (0-5 scale)	Sugar yield (cwt/acre)	oz a.i./ acre	Root fanginess (0-5 scale)	Sugar yield (cwt/acre)
Untreated		3.1	29.2		1.8	48.5
Thionazin granules	9	2.9	45.8***	9	1.4	51.9
Aldicarb granules	16	0.7***	62.2***	7	0.7***	80.2***
" "	7	0.8***	53.7***	5	0.5***	77.4***
	4	1.0***	55.8***	2	0.5***	76.9***
Methomyl solution	40	2.1***	21.6	48	1.2**	64.2*
" "	13	2.0***	38.5*	16	0.7***	71.9***
23 23	4	2.6*	40.4*	5	0.4***	70.4**

 $\| 0-5 =$ scale of increasing root fanginess. *, **, *** Statistically significant improvement in root shape or sugar yield at 5%, 1% and 0.1% levels of probability respectively.

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of methomyl ('Lannate') solution also greatly increased sugar yields in two trials in 1967 (Table 14) but damaged beet in 1968 and 1969. The 1967 trials were with single-row plots, so the yield increases in Table 14 are somewhat exaggerated.

At Docking in 1967, where the soil was infested with *T. cylindricus*, 48 oz methomyl/ acre, sprayed in a 6-inch wide band over the sugar beet rows immediately after sowing, increased sugar yield from $22 \cdot 1$ to $43 \cdot 1^{***}$ cwt/acre (Whitehead, Tite & Fraser, 1970).

Aldicarb granules were applied in the seed furrows at ten sites in 1968 and at nine in 1969; Docking disorder occurred at three in 1968 and all nine in 1969. Averaging all 19 trials, 4, 8 and 16 oz a.i./acre increased yield from 48.9 cwt sugar/acre to 52.3, 53.2 and 54.4 cwt sugar/acre; at the current price of aldicarb its use was justified only at the sites where Docking disorder was severe (Dunning & Winder, 1970). Aldicarb seems not very toxic to *T. anemones*, for treating soil with as much as 100 ppm decreased numbers extracted by only 67% after three weeks (Dunning & Winder, 1969a). However, it seems to prevent the nematodes feeding on roots that have absorbed it from the soil, and this is enough to make seedlings grow more vigorously.

Aldicarb is a strong cholinesterase inhibitor and is therefore hazardous to apply, but small amounts can conveniently be applied at sowing with a granule applicator mounted on the seed drill. Aldicarb thus applied also protects the seedlings from beet leaf miner (*Pegomya betae* (Curt.)) and aphids, and checks the spread of 'virus yellows' virus (Dunning & Winder, 1969a).

Four field trials in 1969 compared 6 gal 'D-D' or 'Telone'/acre, applied 6–8 inches deep in the rows two weeks before or immediately before sowing, with 8 oz a.i. aldicarb/acre applied as granules in the seed furrow during sowing. The average sugar yield from the untreated plots was 50.0 cwt/acre; 'Telone' injected two weeks before sowing or immediately before sowing increased yield to 58.8 and 57.9 cwt/acre respectively, 'D-D' (both times of application) to 57.5 cwt/acre and aldicarb granules to 54.9 cwt/acre. Aldicarb was probably less effective because nitrogen was leached by the excessive rain in May (Cooke, Dunning & Winder, 1970).

Summary

Ectoparasitic nematodes, especially species of *Trichodorus* (stubby root nematodes) and *Longidorus* (needle nematodes), feed on and damage the root tips of sugar beet; Docking disorder is the poor growth of sugar beet resulting from this primary damage. Yield loss does not depend only on the number of nematodes in the soil, but also on other interacting factors, especially soil structure and rainfall, which affect the numbers and activity of the nematodes, the nutrients available to the seedlings and the vigour of root growth. Modern cultural practices, especially the use of herbicides and drilling to a stand probably increase the prevalence and severity of Docking disorder. Approximately 20 000 acres of sugar beet suffered from Docking disorder in 1969, at an estimated yield loss exceeding 50 000 tons of roots.

Damage can be alleviated by correct use of nitrogen, principally by avoiding leaching or replacing the nitrogen lost by leaching, and it can be prevented by nematicides. Fumigating all the top soil with 'D-D' or 'Telone' kills nearly all the nematodes and greatly increases the yield of sugar beet and other crops in the rotation, but is expensive. Small amounts of fumigant or systemic nematicides applied to the sugar beet rows at or before sowing kill most of the nematodes in the rows, or prevent them from feeding on the roots, allow the seedlings to grow vigorously, and can greatly increase yield. 234

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