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Symptom development on two wild, perennial grasses infected by *Peronosclerospora* species (Family Peronosporaceae: the downy-mildew fungi)

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Abstract. The reproductive structures of the downy-mildew fungi, *Peronosclerospora noblei* and *Peronosclerospora eriochloae*, develop only on chlorotic leaves of tall, vegetative tillers of the perennial grasses *Sorghum leiocladum* (wild sorghum) and *Eriochloa pseudoacrotricha* (early spring grass), respectively. They are never found on the leaves of flowering tillers, even when tillers of both types grow from the same tussock. The development of symptoms on infected tillers of both hosts and the morphological and anatomical changes to host tissues on infected tillers are detailed.

Introduction

Many systemic fungal pathogens have been recorded on native grasses in Queensland. Although taxonomic studies have been undertaken on some of these pathogens, the biology of most of them has not been studied. Many of the grasses that have been brought into cultivation, such as sorghum [*Sorghum bicolor* (Moench) L.] and maize (*Zea mays* L.), are annuals and are subject to systemic infection by various pathogens, including downy-mildew fungi. Considerable research has been undertaken on the biology of these pathogens as a response to the threat of economic loss. However, many systemic fungal pathogens of perennial grasses cause little economic loss and are often of limited geographic distribution. As a result, little research has been undertaken on their interactions with grass hosts.

This paper reports on the symptoms caused by downy-mildew fungi on two perennial grasses native to Australia. The first, *Peronosclerospora noblei* (Weston) C.G.Shaw on wild sorghum [*Sorghum leiocladum* (Hack.) Hubb.], was described as *Sclerospora noblei* Weston by Weston (1929, 1942) from material collected by R. J. Noble near Glen Innes, New South Wales (*c.* 29°43′S, 151°43′E). Later, *S. noblei* was placed in *Peronosclerospora* by Shaw (1980). Wild sorghum is confined to the Great Dividing Range, which runs north–south along the east coast of Australia, and to isolated areas of the coastal plains between southern Queensland and northern Victoria (Hubbard 1938). The first report of *P. noblei* from Queensland was by Langdon (1950), who collected frayed leaves (with adherent oogonia of the downy-mildew fungus) of *S. leiocladum* from a site near Hirstglen, southern Queensland (27°49′06″S, 152°06′14″E). Since then, infected tussocks of wild sorghum have been found on basaltic soil at a number of elevated sites in south-eastern Queensland (Ryley 1985). The second, *Peronosclerospora eriochloae* Ryley & Langdon on early spring grass [*Eriochloa pseudoacrotricha* (Stapf ex Thell.) J.M.Black], has characteristics distinct from any valid species of that genus (Ryley and Langdon 2001). Early spring grass is found in all the mainland states of Australia (Vickery 1961). Tussocks of early spring grass infected by *P. eriochloae* have been found at several sites in south-eastern Queensland (Ryley 1985; Ryley and Langdon 2001). Ryley (2001) has given a brief account of the symptomatology of wild sorghum infected by *P. noblei* and has described the relationship between the location and activity of hyphae of the pathogen and symptoms on infected tillers.

Populations of wild sorghum at Hirstglen and early spring grass at Upper Pilton provided an opportunity to compare and contrast the symptoms of the two host–downy mildew fungi interactions under field conditions. Detailed observations on the symptomatology displayed by plants of wild sorghum and early spring grass infected by their respective downy-mildew fungi were made over three consecutive years (1979–1981). The progression of

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symptoms expressed by individual tussocks and by tillers within those tussocks, was followed from the beginning of the summer-growing period through to the winter-dormancy period in each of 3 years. Differences in the anatomical and morphological characteristics of various host organs affected by the two downy mildew fungi were quantified.

Materials and methods

In the late winter (August) of the first year, 20 healthy tussocks and 20 diseased tussocks were selected in a population of wild sorghum growing at a site near Hirstglen, Queensland. Healthy tussocks were designated as those that displayed remnants of flowering tillers only. Some tussocks had remnants of tall, dead tillers on which frayed leaves were evident while others had also remnants of flowering tillers. Each tussock was identified by an aluminium tag attached to a steel peg driven into the ground, the tag bearing data on the tussock's number, the nature of the tussock and the date of selection. Other tussocks were removed from the field site and transplanted to a large garden plot in the grounds of the University of Queensland, St Lucia campus. After transplanting, tussocks were cut back to a short stubble. These transplanted tussocks provided ready access to infected tillers at various stages of development. Over the 3 years of the study, visits were made to the field site at Hirstglen at about fortnightly intervals during the summer months and monthly intervals during the winter months for two purposes.

First, the numbers of flowering tillers and/or diseased tillers on individual marked tussocks were recorded at each visit over the 3 years to study the seasonal behaviour of tillers. To avoid disturbing the structure of the tussock, tillers were not removed from the tussocks, so that the total number of tillers counted at each visit was the sum of tillers surviving from previous recording periods plus the new tillers that had elongated since the previous visit. In this study, a flowering tiller was counted on the date of appearance of its inflorescence and a downy mildew-infected tiller on the date of appearance of the first chlorotic leaf.

Second, measurements and observations on a number of individual tillers were made at each visit to study the development of the symptoms of downy mildew infection. At the beginning of each growing season, 20 infected tillers and 20 flowering tillers were selected on each marked tussock and a small cardboard tag bearing the tiller number was attached to each culm near its base. Diseased tillers were recognised by the production of chlorotic leaves, and healthy tillers by the swelling of the leaf sheath that enclosed a developing inflorescence near the apex of the culm. Tillers of both types were 25–40 cm high at the time of tagging. At each visit, measurements were made of tiller height, leaf number, internode lengths, leaf-sheath length, the length, width and angle of leaf blades, the location and extent of chlorotic tissue and the area where sporulation occurred on leaves of infected tillers.

The morphological characteristics of mature tillers were determined from 50 randomly selected flowering tillers on tussocks with and without downy mildew-infected tillers, and from 50 infected tillers. All tillers still displayed green leaves at the time of collection. The following characteristics were observed and/or measured: tiller height (base to the tip of the inflorescence for flowering tillers and to the tip of the last-formed leaf for infected tillers), number of visible nodes, culm diameter halfway between the 2nd and 3rd nodes, the length and width of each leaf and features of ligule of the widest leaf. Mean values were compared pairwise by the '*f*' test. The anatomical features of the widest leaf and of the culm between the 2nd and 3rd nodes of 10 healthy and 10 infected tillers were determined by cutting transverse freehand sections and staining in safranin and fast green (Johansen 1940). The number and arrangement of vascular bundles was noted. Stomatal densities of the upper and lower epidermis of these leaves were determined by preparing epidermal strips.

A population of early spring grass consisting of both healthy and downy mildew-infected tussocks at a site near Upper Pilton (approximately 5 km from Hirstglen) was chosen for the study. Progressive studies of symptoms and tiller production were carried out, but were hindered by frequent disturbances of the site by grazing domestic stock and by road-building machinery. The methods used during the study were similar to those used for *P. noblei* on wild sorghum, but observations were restricted to six downy mildew-infected tussocks and six healthy tussocks.

Results

Wild sorghum

Characteristics of healthy tussocks

Two types of tillers develop on healthy tussocks of wild sorghum. At any time of the year, there are short vegetative tillers, 30–40 cm high and each with three or four narrow, arching leaves. Although many of these tillers die during winter (May–September), some individuals survive for more than 1 year. During the late-spring and early summer months (October–January), tall flowering culms up to 170 cm high and bearing two to four narrow leaves and a loose terminal red-brown panicle develop (Fig. 1*a*). In each of the three growing seasons of the study, flowering tillers were produced over one short period from late October to late December, the start of that period varying from year to year and depending on the timing of rainfall. These tillers have a short life span (50–70 days), breaking up readily after maturation of the caryopses. Flowering tillers produced early in the season are often necrotic when later-produced flowering tillers are still elongating. In this way, there is a gradual, but steady, replacement of flowering tillers during the growing season.

Both types of tiller arise from tiller bases near the periphery of the tussocks. The centre of a large tussock at, or just below, ground level consists of tightly packed tiller bases and roots, many of which are dead. Tussocks enlarge by repeated production of tillers from axillary buds on the live tiller bases. Necrosis of parts of, or the whole of, certain tiller bases may result in separation of the original plant into several distinct but still closely placed portions, each of which may enlarge in the manner described above. Seedlings of wild sorghum were never observed growing at Hirstglen or any other locality. Disarticulated spikelets sown into sterile potting mix and watered regularly failed to germinate, but a few caryopses (<10%) dissected from such spikelets germinated and grew into mature plants, flowering only when they were at least 1 year old.

Symptoms on downy mildew-infected tussocks

In the very early stages of development, tillers that ultimately display downy-mildew symptoms cannot be distinguished from short, vegetative tillers or flowering tillers. The first sign that a tall-growing tiller is infected is the emergence of a partly chlorotic leaf (Fig. 1*b*). This occurs

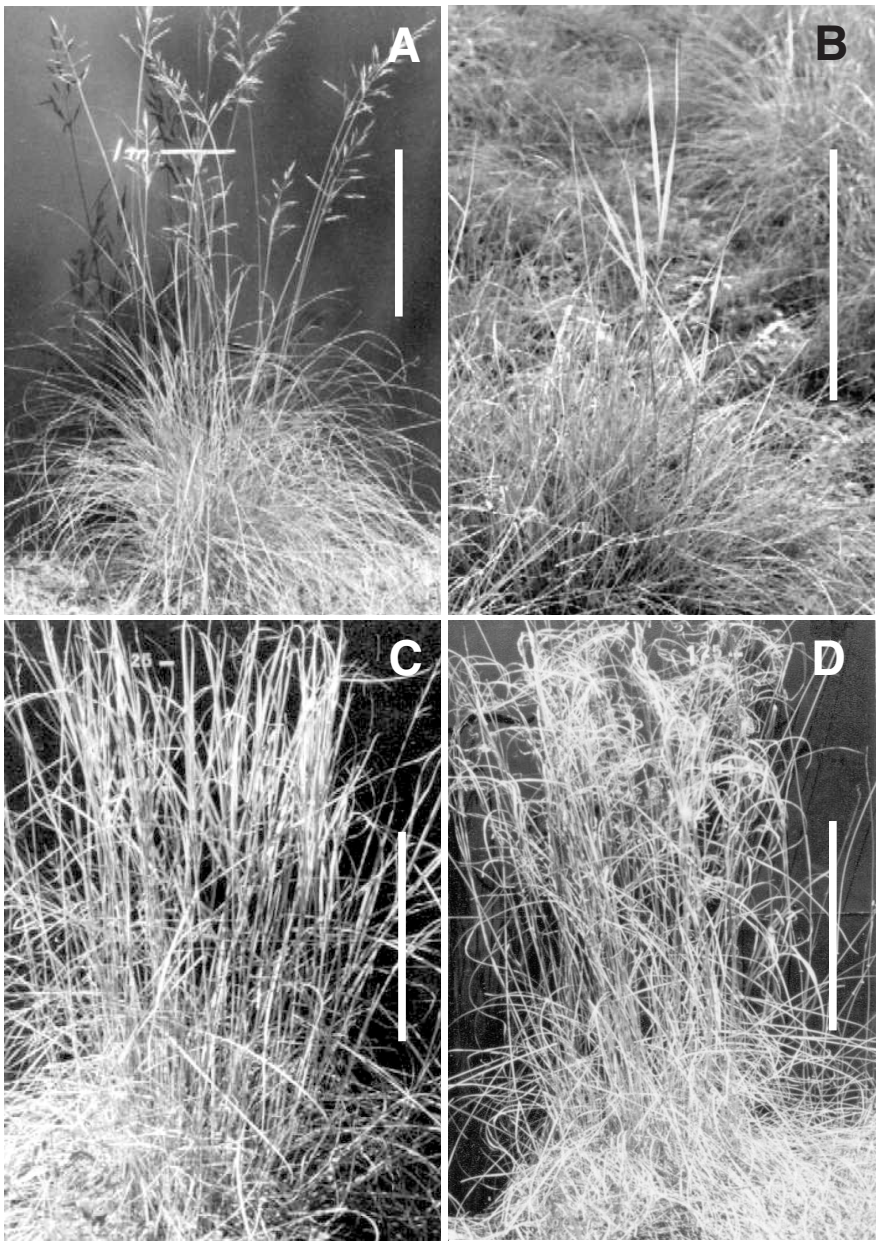

Fig. 1. *Peronosclerospora noblei* on *Sorghum leiocladum*. (*A*) Mature flowering tillers on a healthy tussock; (*B*) chlorotic leaves of a developing, infected tiller; (*C*) mature, infected tillers on a diseased tussock; (*D*) frayed leaves bearing oogonia in upper parts of infected tillers. Scale bars = 50 cm.

when the tillers are 25–40 cm high (measured from ground level to the upper leaf ligule) and already have two to four normal green leaves (hereafter referred to as normal basal leaves), similar to those on both short, vegetative tillers and flowering tillers. These infected tillers are produced at the same time as flowering tillers. On the first chlorotic leaf, chlorosis is confined to the basal half of the leaf blade. The chlorotic area may cover the entire width of the leaf blade with no interruption by green tissue, be confined to one side of the mid-vein, or occur in isolated patches. Chlorosis never occurs on the normal basal leaves of an infected tiller, on the internodes, or on the leaf sheath of the first chlorotic leaf. The blades of leaves (six to eight) produced subsequently are usually entirely chlorotic, even while still within the enclosing leaf sheath. The sheaths subtending the fully expanded chlorotic leaf blades usually remain green, but during the study two leaves were found to have chlorotic sheaths, with the chlorosis extended down the sheath for only

a short distance (2–4 cm). The chlorotic leaf blades (5–9 mm wide) are broader than the first-formed leaves of normal appearance on infected tillers and the leaves of healthy tillers (2.0–3.6 mm wide).

Asexual sporulation is confined to the chlorotic areas of the wide, chlorotic leaves of infected tillers and then on the abaxial surface only. On the first-formed chlorotic leaf, sporulation does not begin until the leaf blade is fully expanded, even though conditions conducive to asexual sporulation may occur before this time. On subsequent leaves, the asexual reproductive structures develop soon after the leaf blades emerge through the surrounding sheaths. For all leaves, asexual sporulation occurs first at the tip and spreads towards the base in a series of increments. For an individual leaf, the increments are not constant, their size depending on the period of time between successive periods of sporulation.

Fifty to sixty days after the development of the first chlorotic leaf, infected tillers reach their maximum height of about 85–160 cm, which is similar to the height of flowering tillers. The last-formed leaves never fully emerge past the enclosing sheaths of the lower leaves and consequently the uppermost leaves on the infected culms exhibit a bunchy-top appearance (Fig. 1*c*). Soon after infected tillers stop growing, the last-formed leaves rapidly necrose while still only partly expanded. The normal basal leaves are necrotic at this time, but on the lowermost three or four chlorotic leaves chlorotic tissue persists at the proximal ends of the leaf blades. The uppermost chlorotic leaves die sooner than the lowermost infected leaves and soon after the blades of these leaves begin to fray. The intervascular tissue disintegrates and the vascular bundles remain as threads to which oogonia containing oospores adhere. Fraying progresses towards the ligule and ultimately the whole leaf blade becomes a mass of intertwined vascular threads (Fig. 1*d*). The parts of the leaf below the ligule (that is, the leaf sheath) never fray. During the winter months, infected tussocks are recognisable by the presence of tall tillers bearing frayed leaves. Because infected tillers have stout stems they are not as easily broken by natural agents as flowering tillers, and so during the winter months the remnants of the tall, infected tillers predominate.

Both infected tillers and flowering tillers develop on some tussocks, the numbers of diseased and healthy tillers varying from tussock to tussock and from season to season in an individual tussock. Short, vegetative tillers identical with those on healthy tussocks are present throughout the year. The asexual and sexual states of *P. noblei* were never found on tall, flowering tillers or on the short, vegetative tillers of healthy or infected tussocks.

Tiller abnormalities

Two types of tiller abnormality were found on approximately 0.5% of downy mildew-infected tillers. In the first type, upper portions of the tillers are twisted and bent, with part of the culm protruding through the uppermost normal leaf sheath (Fig. 2*a*). As the tiller grows, the protruding portion consists of closely placed nodes and associated chlorotic leaves formed into a ring-like structure. The other form of vegetative abnormality is characterised by a number of crowded nodes at the apex of a diseased tiller (Fig. 2*a*). A leaf that is shorter and narrower than chlorotic leaves on normal infected tillers arises from each node. The blades of the leaves on this abnormality are chlorotic only in the interveinal tissue. Structures with an anatomy similar to that of monocotyledonous roots are produced from some of the nodes. Asexual sporulation occurs on the chlorotic areas of the leaf blades from time to time, in a manner similar to that described above for infected tillers without abnormalities. The leaf blades on only the first type of abnormal structure ultimately fray.

Malformed inflorescences

Most of the tall tillers on which there are chlorotic leaves, and later frayed leaves, remain in a vegetative state. A random sample of 100 infected tillers in various stages of development was collected from untagged tussocks and the growing points excised and examined microscopically. In every case, the growing point was vegetative, consisting of a meristem with a row of leaf primordia surrounding the apical meristematic zone. No floral primordia were ever observed.

However, a few infected tillers produce structures that resemble inflorescences. The culms that bear abnormal inflorescences have two or three normal basal leaves and three or four wider upper leaves on which there are fine, chlorotic interveinal streaks. The upper leaves are not as wide as, and do not display the extent of chlorosis exhibited by the uppermost leaves on vegetative, infected culms. Sparse asexual sporulation occurs on these fine, chlorotic streaks when there are suitable environmental conditions. No sexual reproductive structures are formed on any tissue of the tillers. Also asexual sporulation is observed on thin, chlorotic streaks on the outer elements of some of the spikelet-like structures of the abnormal inflorescences.

There are marked changes in the characteristics of inflorescences on downy mildew-infected tillers when compared with normal inflorescences (Table 1). The abnormal inflorescences are twisted, shorter than those on healthy culms and have a disorderly arrangement of branches and racemes. There are also marked changes in the arrangement and composition of the spikelets on those inflorescences. Although under-developed, male reproductive organs, either alone or together with female reproductive organs, are found in some of the spikelet-like structures, no mature caryopses are found in inflorescences on infected tillers.

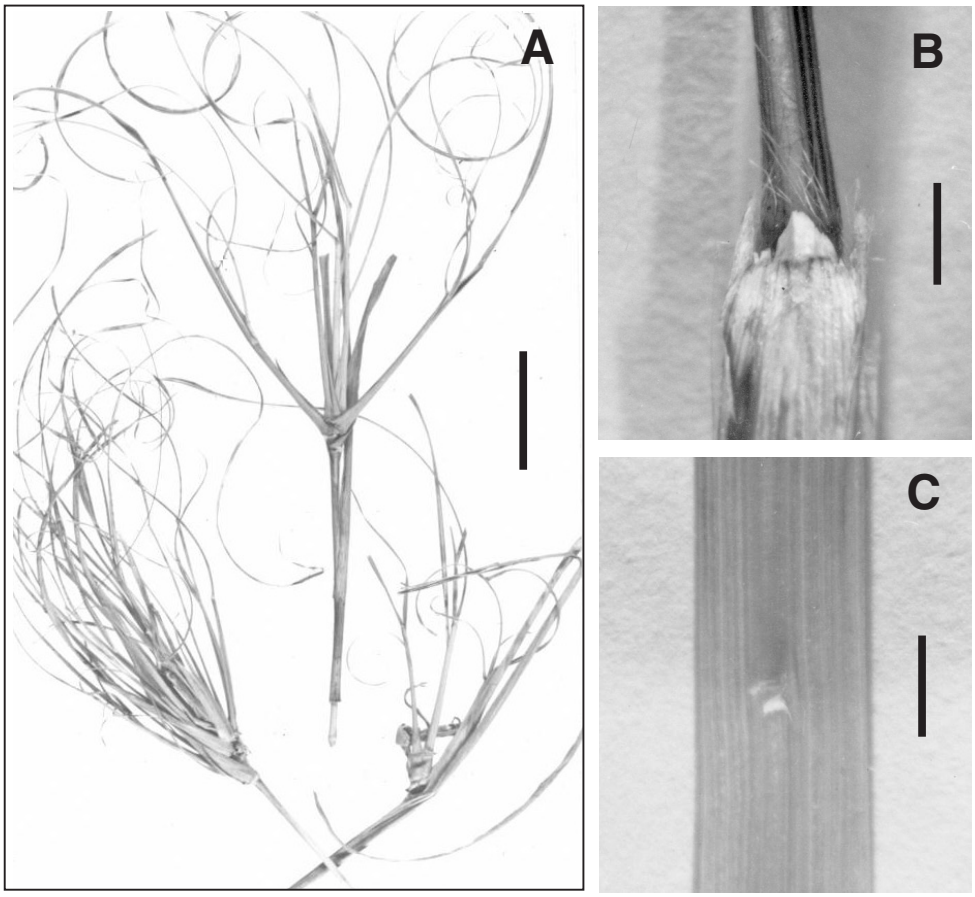

Fig. 2. *Peronosclerospora noblei* on *Sorghum leiocladum*. (*A*) Vegetative abnormalities on infected tillers; (*B*) ligule area of normal leaf; (*C*) ligule area of infected, chlorotic leaf. Scale bar = 10 cm (*A*), 5 mm (*B*, *C*).

Morphological and anatomical changes

There were no significant differences in the number of nodes, height, culm diameter or leaf width of flowering tillers on healthy and infected tussocks of wild sorghum. However, tillers infected by *P. noblei* had significantly more nodes and

Table 1. Characteristics of inflorescences on healthy, flowering tillers and on tillers infected by *Peronosclerospora noblei*, of *Sorghum leiocladum*

Characteristic	Healthy tillers	Infected tillers
Panicle type	Open	Racemose
Panicle length (cm)	15–22	10–15
Peduncle length (mm)	26–65	5–20
Peduncle axis	Straight	Twisted
Spikelet arrangement	Paired, 6–10 per raceme	1–5 per branch
Spikelet length (mm)	6–8	4–23
Spikelet type(s)	Sessile, hermaphrodite, 5 floral elements; pedicillate, male or neuter, 5 floral elements	Hermaphrodite, male or neuter, 2–5 floral elements

Table 2. Comparison of morphological and anatomical characteristics of flowering tillers and of tillers infected by *Peronosclerospora noblei*, of *Sorghum leiocladum*

For each characteristic, the range and the mean (in parentheses) are given. Mean values in each row followed by different letters are significantly different ($P = 0.05$)

Characteristic	Flowering tillers	Infected tillers
Culm		
Node number	2–(3.2)–4a	6–(7.8)–11b
Height (cm)	114–(137.3)–170a	84–(129.5)–162a
Diameter (mm)[A]	1.0–(1.7)–2.5a	1.6–(2.1)–3.0b
No. vascular bundles[A]	53–(58.5)–66 a	55–(60.8)–65a
Leaf blade[B]		
Width (mm)	2.0–(2.8)–3.6a	5–(6.5)–9b
No. vascular bundles	35–(39.6)–49a	62–(69.0)–75b
No. stomata × 10^3 cm^{-2}		
Abaxial surface	16.7–(21.3)–25.3a	14.7–(19.5)–28.0a
Adaxial surface	0.7–(1.9)–2.7a	2.7–(4.2)–6.7b

[A]Measurements taken halfway between 2nd and 3rd nodes.
[B]Measurements taken at the widest point of the widest leaf on each tiller.

wider culms and leaves than flowering tillers (Table 2). Infected, chlorotic leaves had a significantly greater number of vascular bundles than leaves on flowering tillers, but there were no differences in the number of vascular bundles between the culms of flowering and infected tillers. On mature, flowering tillers the angle between the leaf blades and culms lay within the range 45–100°. The angle of normal basal leaves on infected tillers was within this range, but the angle for chlorotic leaves was never greater than 20° from the culm.

On normal leaves on flowering tillers and on normal basal leaves on infected tillers, the ligule area is a zone of morphological discontinuity. The ligule is a membranous, triangular flap 1.5–2.0 mm high and 2.5–3.0 mm wide and two lateral projections 0.5–1.0 mm high and clothed with hairs up to 10 mm long are present on each side of the ligule (Fig. 2*b*). The leaf blade just above the ligule is 1.5–2.0 mm wide and the leaf sheath immediately below the ligule is 4–8 mm wide. In the fully chlorotic leaves, the leaf blade was as wide as, or wider than, the leaf sheath and the ligule was reduced to a small membranous flap 0.8–1.0 mm wide and 1.5–2.0 mm high (Fig. 2*c*). There were no significant differences in the stomatal density on the abaxial leaf surfaces between tiller types, but there were significantly more stomata on the adaxial surfaces of chlorotic leaves than on normal leaves. There was almost five times the number of stomata on the abaxial surfaces of chlorotic leaf blades than on the adaxial surfaces of those leaf blades (Table 2).

Early spring grass

Characteristics of healthy tussocks

During the dormant season (April–August) of early spring grass healthy tussocks consist of only a few short, persistently vegetative tillers, 10–15 cm high, and with two or three leaves each 7.5–15.0 cm long and 3–5 mm wide. In early spring, there is a flush of vegetative growth, and many short vegetative tillers develop. Soon afterwards, flowering tillers are initiated. At first, these are very similar externally to short vegetative tillers, but they form flower primordia when the growing points are a few centimetres above ground level. At that time, there are two to four green leaves, the first one or two of which are fully expanded. After the inflorescence emerges, the tiller rapidly increases in height due to the elongation of the uppermost two or three nodes and the inflorescence peduncle. By the time the flowering tillers reach their ultimate height (up to approximately 100 cm high with four to nine narrow leaves and bearing a panicle of 2 to 10 racemes), the lowermost three or four leaves are entirely necrotic (Fig. 3*a*). The blades, and later the sheaths, of the leaves die, with the lowermost leaves dying before the uppermost leaves.

Just before the inflorescence on the main culm emerges, branches develop at one or more of the lowermost three nodes, pushing their way upwards between the culm and the leaf sheath. When the main culm has reached its full height, the axillary branches are much shorter and have one, two or three leaves. The branches rapidly elongate and an inflorescence emerges through the sheath of its uppermost leaf. The axillary branches ultimately reach a height of up to 70 cm, with the branches formed at the lowermost nodes being longer than those that develop from nodes higher on the culm. Occasionally, a branch develops from the lowermost node on an axillary branch.

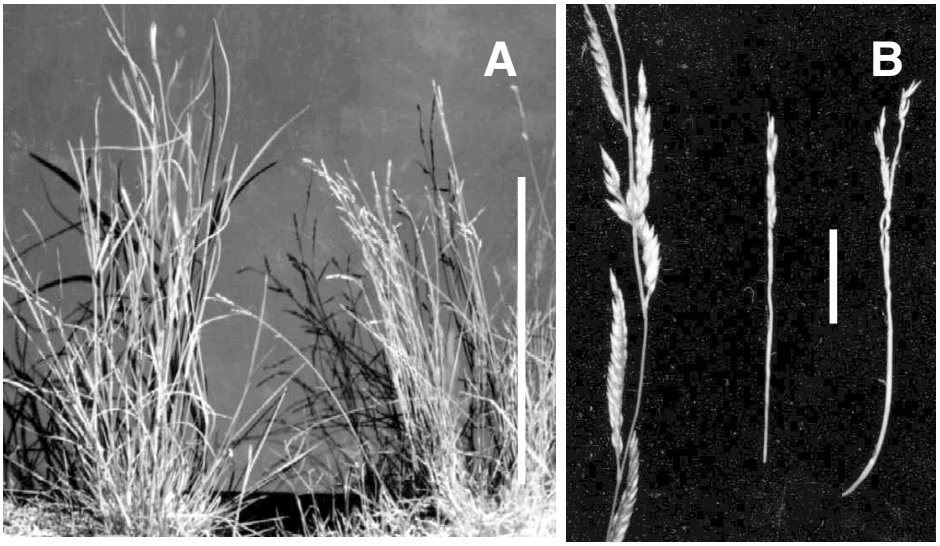

Fig. 3. *Peronosclerospora eriochloae* on *Eriochloa pseudoacrotricha*. (*A*) Left—mature infected tillers on diseased tussock, right—mature, flowering tillers on healthy tussock. (*B*) Left—section of normal inflorescence on healthy tiller, right—abnormal inflorescences on infected tillers. Scale bar = 50 cm (*A*), 10 mm (*B*).

There is a continual production of tillers between September and March, with a few tillers developing in the early part of the growing season and many more tillers developing as the season progresses. Towards the end of summer, the tillers die rapidly and the culms break up. During the winter months, only the basal parts of some of these tillers remain. Short vegetative tillers are present throughout the year and, although some die during winter, many survive from one growing season to the next. A few healthy seedlings of early spring grass were observed at Upper Pilton during January of one summer and consisted of a culm, 15–25 cm high, with three to four green leaves and bearing an inflorescence and shorter vegetative tillers arising from the subterranean portion of the flowering tiller.

Symptoms on downy mildew-infected tussocks

The first evidence that a tiller is infected by *P. eriochloae* is the emergence of a wide, partly chlorotic leaf when the tiller is 10–20 cm high (measured from ground level to the uppermost ligule). This occurs during the same period when flowering tillers are developing. At the emergence of the first chlorotic leaf, one, or less commonly two, leaves similar to those on tall flowering tillers and on short vegetative tillers have already been formed. The term 'normal basal leaves' was adopted for such leaves when the downy mildew of wild sorghum was being discussed. The same terminology is applicable here. On the first chlorotic leaf, chlorosis is confined to the basal portion of the blade. This may extend for the entire width of the blade, be confined to one side of the midvein, or be in the form of irregular patches between the veins. As the tiller elongates, additional leaves whose blades are fully chlorotic emerge through the uppermost leaf sheath. There is never any chlorosis of normal basal leaves, or of the internodes of culms. On a few chlorotic leaves, chlorosis extends from the blades onto the sheaths for up to 2 cm.

When fully expanded, the chlorotic leaf blades are wider (5.0–7.0 mm) than the blades of normal basal leaves on infected tillers (2.0–6.0 mm) and of leaves of flowering tillers (2.5–7.0 mm). They are held at an angle of between 5 and 10° to the culm. When the chlorotic leaves die, the angle of the leaf blade remains unchanged. This contrasts with the normal basal leaves of infected tillers and the leaves on flowering tillers where the angle between the leaf blade and culm decreases from between 20 and 30° to between 5 and 10° as leaves necrose. On infected tillers, the uppermost internodes are never as long as the lowermost internodes, with the result that the chlorotic leaves near the apex of the culm present a bunchy-top appearance.

As the tiller elongates, the first-formed leaves begin to die from the tip towards the base. Twenty-five to 40 days after the first chlorotic leaf becomes evident, the normal basal leaves are becoming necrotic. Before the main culm reaches its full height, there is usually some branching by activation of one or more of the axillary buds at points beyond the first node. The first leaf of a branch is always partly chlorotic, with the chlorosis being confined to interveinal areas. The blades of additional leaves (two or three) are entirely chlorotic.

Asexual sporulation occurs from time to time on both the adaxial and abaxial surfaces of chlorotic leaf blades. On partly chlorotic leaf blades, production of the asexual reproductive structures is confined to the chlorotic areas that may be separated by areas of green tissue. The pattern of asexual sporulation on chlorotic leaves of infected tillers is similar to that on wild sorghum infected by *P. noblei*. On leaves of branches that grow from one or more of the lowermost nodes of the culm, asexual sporulation follows a pattern similar to that on the leaves on the culm itself. No conidiophores develop on the fully green parts of leaf blades that are only partly chlorotic, on the sheaths of leaves with chlorotic blades, or on the normal basal leaves on infected tillers.

Thirty-five to 60 days after the appearance of the first chlorotic leaf, the main culm reaches its full height. At this stage the lowermost four or five leaves are entirely necrotic and the branches that had developed from the lowermost nodes are elongating. The leaves die in progression up the culm, with the uppermost leaf being the last to die. That leaf does not fully emerge and it is the last leaf to die on the main culm. The branches elongate for 20–50 days after all the leaves on the main culm have died, the pattern of leaf necrosis on the branches being very similar to that on the main culm.

The pattern of fraying on the leaves of infected tiller is different from that of leaves on infected tillers of wild sorghum. Before the main culm reaches its full height and while there are expanding chlorotic leaves at the apex, the second or third mildewed blade on the culm begins to fray. Fraying of the leaf tissue starts at a point 2–7 cm from the tip of the blade and gradually extends towards the base of the leaf blade. When fraying commences near the tip of the leaf there is often a chlorotic area near the base of the leaf blade. Ultimately, almost the entire leaf blade frays, with oogonia adhering to the remnants of the vascular bundles. Fraying extends as far as the ligule. As the tiller elongates, the leaf blades fray in succession, acropetally. The pattern of fraying on those leaves is the same as described above.

The frayed leaves on infected tillers of early spring grass never tangle as do the leaves on tillers of wild sorghum infected by *P. noblei*. Instead, they retain the same general outline that they had while chlorotic. Although the vascular bundles have separated from one another almost along the entire length of the leaf blade, there is a short length of leaf at the tip (usually <1 cm) where no separation of the vascular bundles from the interveinal tissue has occurred. During the winter months, tillers bearing frayed leaves are evident on infected tussocks, but tillers that had flowered disintegrate rapidly soon after they die.

Flowering tillers very similar to those on healthy tussocks often develop from infected tussocks, but then in no regular proportions. Short, vegetative tillers similar to those on healthy tussocks are present on infected tussocks throughout the year. No reproductive structures of *P. eriochloae* develop on the leaves of short, vegetative tillers or of tall, flowering tillers, even those on tussocks that produce infected tillers.

A large number of seedlings displaying symptoms of downy mildew infection were observed at the same time as the healthy seedlings described in the previous section. The infected seedlings consisted of one or two culms up to 15 cm high with one or two green, basal leaves and one or two chlorotic leaves. On the lowermost chlorotic leaf, chlorosis was confined to the basal part of the leaf blade, but the other leaf was entirely chlorotic. Remnants of the conidiophores and conidia of *P. eriochloae* were found on both surfaces of the chlorotic leaf blades.

Malformed inflorescences

Structures resembling inflorescences were found in the apical parts of approximately 30% of infected tillers on tussocks of early spring grass during the study. Most of these inflorescence-like structures are inconspicuous because they did not extend very far beyond the uppermost leaf sheath. The peduncles of inflorescences on healthy, flowering tillers are up to 40 cm long and are much longer than the uppermost leaf sheath. On diseased tillers, the peduncles of the abnormal inflorescence are no more than 1.5 cm long. Consequently, the structure does not stand very far above the uppermost leaf sheath. The normal inflorescence is a narrow panicle, up to 16 cm long, consisting of 2–10 racemes, each up to 10 cm long and bearing up to 20 pairs of spikelets on short pedicels. Abnormal inflorescences are 1–6 cm long with two to five short 'racemes' 0.3–2.5 cm long, each of which bears up to 10 spikelet-like structures (Fig. 3*b*).

The spikelets on normal inflorescences are 4.5–6.0 mm long, 1.0–1.5 mm wide and consist of a lower, sterile floret and an upper, hermaphrodite, fertile floret. On abnormal inflorescences there is a wide variation in the size and composition of the spikelet-like structures. Some of them retain all the elements of spikelets on normal inflorescences, but are smaller than normal spikelets. Others are reduced to small membranous flaps less than 0.5 mm long each with a rounded apex on which there were a number of swellings. Although rudimentary male and female reproductive organs were found in some of the larger spikelet-like structures, no mature caryopses were found in abnormal inflorescences.

Morphological and anatomical changes

On early spring grass, there were no significant differences in morphological features between flowering tillers on healthy and infected tussocks. However, infected tillers were significantly shorter, had more nodes, thicker culms and wider leaves than flowering tillers (Table 3). The numbers of vascular bundles in flowering and infected culms were not statistically different, but there were significantly more vascular bundles in chlorotic leaves than in the normal, green leaves. The upper, chlorotic leaf blades were subtended at 5–10° to the culm and this angle remained unchanged after the leaves die. The blades of normal basal leaves of infected tillers and the leaves on flowering tillers were subtended at 20–30° to the culm which decreased to 5–10° as leaves necrosed. The stomatal densities on the abaxial and adaxial leaf surfaces of chlorotic, infected leaves and of normal leaves were similar.

Table 3. Comparison of some morphological and anatomical characteristics of flowering tillers and of tillers infected by *Peronosclerospora eriochloae*, of *Eriochloa pseudoacrotricha*

For each characteristic, the range and the mean (in parentheses) are given. Mean values in each row followed by different letters are significantly different ($P = 0.05$)

Characteristic	Flowering tillers	Infected tillers
Culm		
Node number	2–(3.8)–6a	4–(6.6)–9b
Height (cm)	36–(60.8)–97b	43–(55.3)–71a
Diameter (mm)[A]	0.6–(1.1)–3.6a	1–(1.4)–2b
No. vascular bundles[A]	55–(61.7)–67a	58–(65.2)–77a
Leaf blade[B]		
Width (mm)	2.5–(3.6)–7.0a	5–(6.0)–7b
No. vascular bundles	72–(77.6)–80a	82–(89.6)–100b
No. stomata × 10^3 cm^{-2}		
Abaxial surface	7.1–(10.8)–14.4a	7.3–(10.2)–14.0a
Adaxial surface	7.3–(10.9)–13.8a	7.3–(11.3)–13.4a

[A]Measurements taken halfway between 2nd and 3rd nodes.
[B]Measurements taken at the widest point of the widest leaf on each tiller.

There were changes in the ligule area similar to those on chlorotic leaves on tillers of wild sorghum infected by *P. noblei*. The sheaths of normal leaves are always 0.5–1.0 mm wider than the blades and the ligule is a row of cilia approximately 1 mm high. The ligule region on the first chlorotic leaf of an infected tiller of early spring grass is very similar to that on normal leaves, but on subsequent chlorotic leaves, the leaf blade immediately above the ligule is 1.0–1.5 mm wider than the leaf sheath directly below the ligule. The row of short cilia is present on all leaves.

Discussion

Kenneth (1966) reported that plants of *Sorghum halepense* (L.) Pers. systemically infected by *P. sorghi* did not differ morphologically from nearby healthy plants. In this paper, it has been demonstrated that the reproductive structures of two *Peronosclerospora* species develop on tillers that differ in many respects from the short, vegetative tillers and the tall, flowering tillers of their respective hosts. For both downy mildew fungus–host combinations, infected tillers have more nodes, wider leaves (related to more vascular bundles) and thicker culms than healthy, flowering tillers. An increase in the culm diameter of infected tillers has been

reported for *Peronosclerospora maydis* (Racib.) Shaw on maize (Mikoshiba 1978) and *Sclerophthora macrospora* (Sacc.) Thirum., Shaw & Naras. on *Dactyloctenium aegyptium* (L.) Beauv. (Sivaramakrishna and Sullia 1978), while a decrease has been noted for others, such as *Peronosclerospora sacchari* (Miyake) Shirai & Hara on sugarcane (*Saccharum officinarum* L.) (Leece 1941) and *P. sorghi* on sorghum (Bain and Alford 1969). Similar differences in the width of invaded leaf blades of different hosts have been noted. Leece (1941), Steindl and Steib (1961), Safeeulla (1976*a*) and Mikoshiba (1978) reported that leaves on infected tillers were narrower than leaves on healthy tillers for some downy mildew fungus–host combinations (*P. sacchari* and *S. macrospora* on sugarcane, *S. macrospora* on *Eleusine corocana* (L.) Gaertn. and *P. maydis* on maize), whereas Akai and Fukutomi (1966) reported that infected leaves were wider on rice (*Oryza sativa* L.) plants infected by *S. macrospora* than those on healthy plants. The only reports of differences in node number are those of Broyles and Grogan (1962) and Vakili and Schafer (1955) who stated that the increase in height of maize tillers infected by *S. macrospora* and of oats infected by *P. sorghi*, was due to an increase in node number.

There were differences in the height of infected tillers compared with that of healthy tillers between the two grasses studied in Queensland. Infected tillers of wild sorghum were similar in height to healthy flowering tillers, while those of early spring grass were significantly shorter than flowering tillers. These differences in height for the two tiller types have been reported for other downy mildew fungus–host combinations. Infected tillers have been reported to be taller, such as *P. maydis* on maize (Mikoshiba 1978), *P. sacchari* on sugarcane (Leece 1941) and *S. macrospora* on oats (*Avena sativa* L.) (Broyles and Grogan 1962), or shorter, such as *S. macrospora* on rice (Akai and Fukutomi 1966) and *E. corocana* (Safeeulla 1976*a*), than healthy tillers. Clearly, the symptoms expressed by grasses infected by different downy mildew fungi vary.

Chlorotic leaves on infected tillers of both wild sorghum and early spring grass are held in an upright manner, in contrast to the green leaves on flowering tillers and in the lower part of infected tillers. The differences in the angle of leaf blades on flowering and infected tillers are related to changes in the anatomy and morphology of the leaves, particularly in the ligule region. On leaves of flowering tillers of wild sorghum the ligule area is a zone of morphological discontinuity, with the result that leaves are usually held at a large angle from the culm. On the other hand, there is no morphological discontinuity between the sheath and blade on wide chlorotic leaves on infected tillers, which are held in an upright manner. The combination of morphological changes in the culm (more nodes, but no increase in height) and leaves (wider than normal leaves) results in the distinctive 'bunchy-top' symptoms of downy mildew infection on both grasses in the field. Although similar symptoms have been reported for other downy mildew fungus–host combinations, this is the first report of the influences of morphological and anatomical changes on this type of symptom for a graminicolous downy mildew fungus.

Most tillers of wild sorghum and early spring grass infected by *P. noblei* and *P. eriochloae*, respectively, remain vegetative. There have been other reports that tillers of some grasses infected by various downy mildew fungi remain vegetative (Thirumalachar and Whitehead 1952; Ullstrup 1955; Tarr 1962; Sun 1970). Some of these authors have used terms such as 'sterile' to describe these tillers, but gave no indication whether these tillers bore rudimentary inflorescences or inflorescence initials that did not develop past that stage. The term 'sterile' may refer to the non-fertile state of the inflorescence, or to the absence of an inflorescence. Several types of vegetative-tiller abnormalities were observed on infected tillers of wild sorghum, a condition which has also been reported on several grasses infected by *S. macrospora* (Ullstrup and Sun 1969; Safeeulla 1976*a*). The tiller abnormalities were never observed on short vegetative tillers, or on healthy flowering tillers of either Queensland grass, suggesting that the presence of the downy mildew fungi affected the development of some infected tillers.

Kenneth (1966) reported that the size and morphology of panicles on plants of *Sorghum halepense* infected by *P. sorghi* were similar to those on healthy plants. However, more commonly, inflorescences on tillers infected by downy mildew fungi are abnormal in some way. Inflorescence abnormalities have been reported for various hosts infected by *P. sacchari* (Leece 1941; Sun 1970), *P. sorghi* (King and Webster 1970), *Sclerospora graminicola* (Sacc.) Shrot. (Safeeulla 1976*a*) and *S. macrospora* (Miles and Epps 1942; Ullstrup 1950; Whitehead 1958; Safeeulla 1976*a*). All involve the proliferation of the floral elements into leaf-like elements, resulting in a conversion of the ordered panicle into a brush-like structure, often without caryopses. The frequency of this symptom for some downy mildew fungus–host combinations is reflected in their common names, for example, crazy top of maize (caused by *Sclerophthora macrospora*) and green ear disease of pearl millet (caused by *Sclerospora graminicola*). By contrast, abnormal inflorescences developed only occasionally on infected tillers of the two grasses in this study.

It is highly likely that the presence of the downy mildew fungi in the two grasses may have brought about changes in the plant's growth-regulation processes. The role of growth regulators in pathogen–host interactions is well established (Sequeira 1973). However, this aspect has been studied for only a few graminicolous downy mildew fungi, and then in little detail. Rai and Sinha (1968) working with *S. graminicola* on *Pennisetum americanum* (L.) K.Schum. and Safeeulla (1976*a*) working with *S. macrospora* on

E. corocana found higher concentrations of auxins in proliferated inflorescences on infected tillers than in healthy flowering tillers. Tarr (1962) suggested that growth regulators, for example gibberellins, might cause abnormal tiller elongation ('jump-up') in sugar cane infected by *P. sacchari*. Growth regulators have been implicated in the stunting of sunflower (*Helianthus annuus* L.) plants infected by the downy mildew fungus *Plasmopara halstedii* (Tarl.) Berl. & De Toni (Benz and Spring 1995). An auxin-metabolising oxidase was found in infected plants but not in healthy plants, and growth in stunted, downy mildew-infected plants was stimulated with exogenously applied gibberellic acid, but not with auxin. Also, the changes in growth regulators that lead to the predominantly vegetative condition of downy mildew-infected tillers are unknown. The two downy mildew fungus–perennial grass combinations studied in southern Queensland would be ideal for studies on the relationships between growth regulators and changes in the host due to infection by a systemic pathogen.

The first sign for a tiller of a grass being systemically infected by a downy mildew fungus is the appearance of a partly chlorotic leaf. Kenneth and Klein (1970) reported that for sorghum systemically infected by *P. sorghi*, symptoms may appear on the first true seedling leaf or be delayed until the ninth leaf. Similar delays in disease expression have been reported by Weston (1920, 1923), Leece (1941), Dalmacio and Exconde (1970), Sun (1970) and Inaba *et al.* (1980*a*) for various downy mildew fungus–cultivated grass combinations. The only report of this feature on a native grass has been for the *Setaria magna* Griseb. infected by *Sclerospora graminicola* (Weston and Weber 1928). In my studies, a similar delay in symptom development was observed on infected tillers of wild sorghum (3rd to 5th leaf) and early spring grass (2nd or 3rd leaf). In the case of wild sorghum, the delay has been demonstrated to be due to the delay in invasion of the leaf primordia in the growing point of the tiller by hyphae of *P. noblei* (Ryley 2001). On both hosts, the first leaf to display symptoms of infection often shows partial chlorosis, the chlorosis being restricted to the basal half of the leaf blade. This feature has also been reported for other graminicolous downy mildew fungi, such as *P. maydis* on maize (Inaba *et al.* 1980*a*), *P. sorghi* on sorghum (Frederiksen *et al.* 1973) and *S. graminicola* on *Setaria magna* (Weston and Weber 1928).

The patterns of asexual and sexual sporulation on chlorotic leaves of infected tillers have rarely been documented. However, the asexual sporulation pattern on an infected leaf is the same for those downy mildew fungus–grass combinations that have been studied. Conidiophores (and conidia) develop first at the tip and progress in increments towards the base (Hughes and Robinson 1961; Inaba *et al.* 1980*b*; present study). Asexual sporulation occurs on both leaf surfaces on infected, chlorotic leaves of early spring grass, as reported for *Peronosclerospora philippinensis* (Weston) C.G.Shaw on maize (Dalmacio and Exconde 1970), *P. sacchari* on maize (Sun 1970) and sugarcane (Leece 1941), and *P. sorghi* on maize and sorghum (Safeeulla 1976*a*, 1976*b*). By contrast, conidiophores develop only on the abaxial surfaces of infected leaf blades of wild sorghum, a characteristic reported for *P. philippinensis* on sugarcane (Chona and Suryanarayana 1955), *P. sorghi* (sic) on *Heteropogon contortus* (L.) Beauv. ex Roemer & Schultes (Dange *et al.* 1974), and *S. graminicola* on *Setaria magna* (Weston and Weber 1928). The stomatal densities on the adaxial and abaxial surfaces of infected leaves of early spring grass are similar, whereas for infected leaves of wild sorghum there are many more stomata on the abaxial surface than on the adaxial surface. For these two grasses, there appears to be a close relationship between stomatal density on the adaxial and abaxial surfaces of infected leaves and asexual sporulation, which may explain conflicting reports for other downy mildew fungus–host combinations.

Leaf shredding due to the development of oogonia has been reported for many downy mildew fungus–grass combinations. There have also been reports of oogonia of some species, namely *P. sorghi*, *S. graminicola* and *P. sacchari*, forming in leaf blades of maize but causing no leaf shredding (Kenneth 1975*a*, 1975*b*; Mukerji and Holliday 1975). Leaf blades of other grasses infected by these three species have been reported to fray (Leece 1941; Safeeulla 1976*a*). Certain aspects of the host's leaf morphology and anatomy, such as the extent of intervascular parenchyma in leaf blades, may have an influence on whether or not leaves fray. The only report of the pattern of fraying on leaves of infected tillers is that of Weber and Weber (1928) for *S. graminicola* on *Setaria magna*. They noted that the older, lower infected leaves frayed first, soon after they fully expanded, and subsequent leaves frayed in a similar manner. On early spring grass, the second or third infected leaves fray while the tiller is still elongating and later-formed infected leaves fray in progression as they develop. However, on wild sorghum fraying commences in the uppermost leaves of the tiller. The reasons for this difference in fraying pattern between the hosts are unknown, but the combination of leaf blade anatomy and the relative crowding of oospores in the intervascular parenchyma in leaves of different ages may play a role. Fraying starts at or near the tip of the leaf blade and progresses towards the ligule, despite differences between hosts with respect to the first leaf to fray. Ryley (2001) and Inaba *et al.* (1980*b*) have correlated this feature of sexual sporulation with changes in the morphology of hyphae in the leaf blade.

Field recognition of mildewed tussocks of wild sorghum or early spring grass during summer is largely dependent on there being chlorotic leaves, usually held erect on stout-stemmed tillers. For both grasses, infected tillers and flowering tillers develop year after year and often on the

same tussock, a feature reported in cultivated, annual grasses (Mackie 1930; Leece 1941; Miles and Epps 1942) and in wild, perennial grasses (Seminiuk and Mankin 1964; Dange *et al.* 1974) infected by various downy mildew fungi. Tiller production in wild sorghum is restricted to one short period in early summer, while that of early spring grass occurs throughout the summer months. Ryley (1985) considers that the pattern of tiller production in both grasses is related to environmental factors, particularly rainfall and, consequently, soil moisture. Clearly, the response of different grass species to external factors varies. In addition, the onset and pattern of tiller production in a population of a particular grass varies from year to year, as does the ratio of the tiller types in individual tussocks. Ryley (2001) demonstrated that the location and activity of hyphae of *P. noblei* in tiller buds of tussocks of wild sorghum determined which tiller buds were invaded and subsequently developed into systemically infected tillers, and which were not invaded. It is highly likely that the activity of hyphae in the tiller bases and the development of tiller buds will vary from year to year depending on environmental conditions, resulting in the differences in tiller production. Therefore, studies on the symptomatology of plants infected by perennial pathogenic fungi should not be restricted to one short period in a year or to only one year.

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