Root Cortical Death in Relation to Infection of Kentucky Bluegrass by *Phialophora graminicola*

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ABSTRACT

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The influence of temperature and shading on natural autolysis of nuclei in root cortex cells, a process called root cortical death, was examined in Merion Kentucky bluegrass (*Poa pratensis*). The process was also studied in four cultivars (Adelphi, Merion, Nassau, and Nugget) of Kentucky bluegrass grown at three temperatures and two light intensities, in the presence or absence of the high-temperature root-infecting pathogen *Phialophora graminicola*. The magnitude of root cortical death in seedlings differed for each cultivar × temperature × light intensity interaction. The process generally occurred faster at 29 C than at 14 or 24 C, and shading reduced the rate of anucleation at 29 C in all cultivars except Adelphi. Numbers of functional nuclei in root cortices were inversely correlated ($P = 0.05$) with percentages of root area colonized by the pathogen and with degree of root blackening and directly correlated with quality of turfgrass foliage. Root cortical death assessments in Kentucky bluegrasses may be useful in breeding and selecting cultivars with improved resistances to root pathogens and environmental stresses.

Additional key words: Fusarium blight, summer patch.

Nonpathogenic lysis of nuclei in the cortex cells of roots has been termed root cortical death (17). The natural senescence in root cortices has been studied mostly in cereal grains (12,13,17) but apparently also occurs in other grasses (4,11). Root cortical death is a highly regulated process, occurring first in the epidermal layer, then continuing, one cortical layer at a time, toward the endodermis (17). Numbers of dead cortical cells increase with increasing distance from the root apex, but cells of the innermost cortical layer and the endodermis often retain their nuclei much longer than cells of the epidermis and outer and middle cortex (17). The intensity of light on wheat foliage modifies the rate of anucleation in cortices of roots (17).

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Nuclear staining techniques are used to demonstrate the occurrence of root cortical death (12,13). Although the process is closely associated with autolysis of nuclei, the death of epidermal and cortical cells is not visually apparent. The roots retain their white color and integrity for many days or weeks after anucleation has occurred. Wheat cortices have been shown to become anucleate on root segments as young as 11 days, even when conditions were considered favorable for growth of wheat roots (17).

Infection of wheat roots by the take-all fungus, *Gaeumannomyces graminis* (Sacc.) Arx & Olivier var. *tritici* Walker, is enhanced by death of root cortical cells (7). *Phialophora graminicola* (Deacon) Walker (26) has an ectotrophic growth habit similar to that of *G. g.* var. *tritici* but is considered incapable of penetrating cortical cells that possess functional (staining) nuclei and of penetrating the endodermis of living wheat and grass roots (6,14). For this reason,

P. graminicola has been considered an avirulent, nectotrophic fungus capable of acting as a biological control agent against take-all on cereal grains (1,19).

Summer patch (a component of Fusarium blight syndrome) of Kentucky bluegrass (*Poa pratensis* L.) in New York was recently attributed to pathogenesis by *P. graminicola* (21,22). The disease appears during hot weather (2,5). Contradictory reports of the fungus being avirulent in Europe and virulent in North America appear to be related to the temperature at which the studies were conducted. *P. graminicola* is a virulent root pathogen at temperatures above 24 C and an avirulent one at 14 C (24,25). All studies in Europe were conducted at less than 20 C, except one at 22 C.

The relationship between root cortical death and infection by *P. graminicola* needs to be reevaluated under environmental conditions that favor pathogenesis by this fungus. Temperature is of greatest importance, but it is also reported that Fusarium blight is seldom observed in shaded areas (2). Light intensity affects the rate of anucleation in wheat roots (17) and many physiological processes in turfgrass plants (27).

We conducted studies to determine whether the rate of root cortical death in four cultivars of Kentucky bluegrass is influenced by light intensity and temperature and if a relationship exists between amount of root cortical death and extent of root colonization by *P. graminicola*.

MATERIALS AND METHODS

Temperature. Effects of temperature on root cortical death in the Kentucky bluegrass cultivar Merion were studied at 14, 24, and 29 C. Plants were grown in a 3:2 (v/v) mixture of soil and sand. The soil was a Chenango very gravelly loam (loamy, skeletal, mixed, mesic Typic Dystrochrept, pH 5.9, containing 2.7% organic matter and 19, 145, 77, and 1,000 μg of extractable P, K, Mg, and Ca, respectively, per gram of soil). The soil was passed through a screen to remove stones and most plant debris, mixed with sand, steam-pasteurized at 60–70 C for 30 min to kill pathogenic agents, dried for 3 days on an open bench, and stored for at least 3 wk before use in experiments. About 75–100 seeds were placed on the surface of the pasteurized soil in 8-cm-diameter clay pots, then covered with a thin layer of sterile gravel. Seeds were preimbibed in a cold running water wash for 24 hr to accelerate seedling establishment (18). Treated seeds were then air-dried at room temperature and refrigerated until used. Three pots of seedlings were incubated in controlled-environment chambers at 14, 24, or 29 C with 14-hr photoperiods and photon flux densities of 280, 275, and 235 μEin/m^2/sec, respectively.

Seedlings were watered once daily, fertilized weekly with a water-soluble solution of 10-10-10 NPK analysis, and left unmowed because previous evidence (23) suggested that mowing accelerates the rate of root cortical death. The extent of root cortical death was evaluated as described later. An analysis of variance was made on the data to determine if treatments differed; if so, further separations of means were made by comparing their confidence intervals (Minitab, version 81.1, Pennsylvania State University).

Temperature and light intensity. Procedures used for the temperature study also were used to determine the effect of shading on root cortical death at 14, 24, and 29 C. Three pots of seedlings were grown under a cheesecloth canopy and a parallel set was grown in full light. The canopy consisted of a double layer of cheesecloth suspended 10 cm above the top of the pots and completely enclosing the sides. Light intensities for the shaded seedlings were 40–47% of the unshaded intensity in each chamber, i.e., 120, 110, and 110 μEin/m^2/sec in the 14-, 24-, and 29-C chambers, respectively. The effects of treatments and their interactions on root cortical death were evaluated by conducting a two-way analysis of variance on the data.

Fungal colonization. The experiment to study the effect of temperature and light intensity on colonization of seedling roots by *P. graminicola* was conducted at the three temperatures and two light intensities described. Inoculum consisted of perennial ryegrass (*Lolium perenne* L.) grains that had been autoclaved, colonized by an isolate of *P. graminicola*, then dried. Before the pots of Kentucky bluegrass were seeded, five seeds of inoculum were placed 1.5 cm deep in each pot, with one seed placed in the center of the pot and the others equidistant from each other and 1 cm from the pot wall. The effects of treatments on root cortical death and on the rate of colonization of cortical cells by the fungus were determined. These procedures were also used to determine root cortical death rates in relation to cortical root rot on 25-day-old root segments of the Kentucky bluegrass cultivars Adelphi, Merion, Nassau, and Nugget. Measurements included the number of stainable nuclei, the percentage of root surface colonized by *P. graminicola*, the intensity of cortical root rot (1–9 scale: 1 = completely blackened root, 4 = evidence of vascular discoloration, 9 = white roots devoid of fungal colonization), and the foliar quality (1–9 scale: 1 = dead plant, 4 = lower limit of visually acceptable quality, 9 = vigorous growth and high quality).

Assessment of root cortical death. Because the extent of root cortical death is known to be influenced by the age of root segments sampled (17), it was important that all root segments sampled were of known age. We therefore "calibrated" the developmental stages and growth rates of roots under all conditions in which they were to be studied. Individual plants were removed from the soil mixture on alternate days, washed, and examined under a dissecting microscope at 20× magnification. The timing of adventitious root initiation and the growth rate were determined.

Root cortical death was determined at two points on adventitious roots 18 days after these roots had begun to grow. Three plants from each pot were removed from the soil, washed, placed in a shallow layer of water, and viewed at 10× magnification. The first initiated adventitious root from each plant was selected for assessment and severed from the plant at the crown. Nine root samples were examined from all treatments except the temperature × shade × *P. graminicola* interaction study, in which 10 roots were selected; five roots were colonized by *P. graminicola* and five were free from fungal colonization.

Cell viability was assessed with the fluorescent nuclear stain acridine orange (12). Whole roots were hydrolyzed for 5 min in 3% hydrochloric acid in 95% ethanol, twice rinsed for 2 min in a phosphate-citrate buffer at pH 3.8, stained for 15 min in 0.001% acridine orange in buffer, and again twice rinsed for 2 min in the buffer. The roots were then whole-mounted in buffer on microscope slides and examined under a Zeiss Universal microscope, using epifluorescent microscopy, magnification of 625×, exciter filter B63 (II), suppressor filter K510, and barrier filters 50/44.

All nuclei that fluoresced (green-yellow) were considered to be functional (13). The number of functional nuclei per microscope field was counted in each of the three cell layers surrounding the stele. This count was made on 2-day-old segments near the root apex (about 1 cm from the apex) and on 18-day-old segments 0.25 cm from the point of root origin. Focusing through cell layers in the whole mounted roots was achieved by using the fine adjustments, as described by Holden (13).

RESULTS

Temperature. The temperature of incubation significantly influenced the number of fluorescing nuclei in apical and coronal regions of Merion Kentucky bluegrass roots (Table 1). The number of nuclei in each cortical layer was lowest at 29 C (Fig. 1); this was especially pronounced in the cortical layer nearest the endodermis.

Temperature and light intensity. The influence of temperature on the number of functional nuclei in the root cortex was very pronounced in Merion Kentucky bluegrass, and the effect of light was significant ($P = 0.05$) in the apical region of roots but not near the crown (Table 1). An interaction of light intensity with temperature was highly significant in the apical region of roots and less pronounced in the coronal region. At 14 C in the innermost cortical layer, the number of functional nuclei was lower in shaded plants than in unshaded plants (Fig. 2). The opposite relationship occurred at 24 C, in that functional nuclei in the innermost layer

were more numerous in the roots of shaded than in unshaded turfs. At 29 C, a strong effect of shading was noted near the root apex, with the roots of unshaded plants having many more functional nuclei than those of shaded plants. This effect was again most apparent in the cortical layer nearest the stele. Shading had no effect on the oldest segments of adventitious roots grown at 29 C; functional nuclei were scarce in roots of shaded or unshaded plants.

Fungal colonization. Results of this study were limited to observations made at 24 and 29 C because *P. graminicola* did not colonize adventitious roots of Merion Kentucky bluegrass plants grown at 14 C. The influence of temperature and light on root cortical death was again demonstrated (Table 1). More important, however, was a strong effect of root colonization by *P. graminicola*. The number of functional nuclei was much lower in roots colonized by the fungus than in apparently equivalent segments that were not colonized (Fig. 3).

TABLE 1. Significance levels for main treatments and their interactions for experiments conducted to determine if rate of root cortical death in four cultivars of Kentucky bluegrass is influenced by light intensity and temperature and if amount of root cortical death and extent of root colonization by *Phialophora graminicola* are related

Experiment	Treatment variable[a]	df	Nuclei[b] Apices	Nuclei[b] Crowns
Temperature	T	2	**[c]	**
Temperature × light	T	2	**	**
	L	1	*	ns
	T × L	2	**	*
Infection by *P. graminicola*	T	1	*	**
	L	1	*	*
	C	1	**	**
	T × C	1	ns	*
	L × C	1	*	*
	T × L × C	1	*	ns
Cultivars	T	2	...[d]	**
	L	1	...	**
	Cv	3	...	**
	T × Cv	6	...	**
	L × Cv	3	...	*
	T × L × Cv	6	...	**

[a] T = temperature, L = light, C = colonization, Cv = cultivars.
[b] Functional nuclei per microscope field in cortical cells.
[c] ** ($P = 0.01$), * ($P = 0.05$), ns ($P > 0.05$).
[d] Not evaluated.

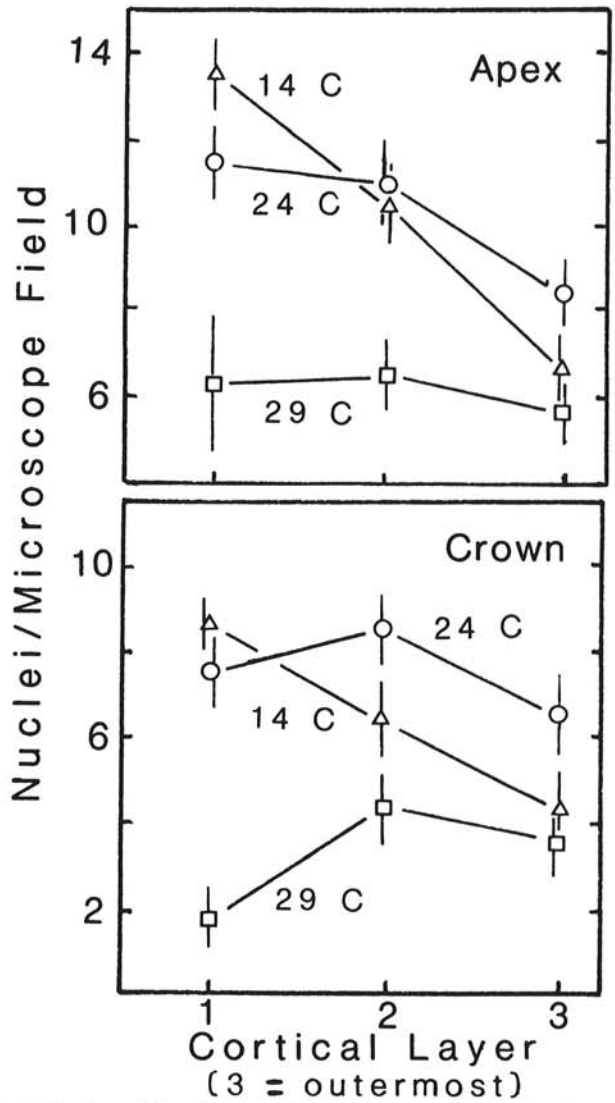

Fig. 1. Numbers of functional nuclei per microscope field in three layers of cortical cells near the apices and crowns of 18-day-old Merion Kentucky bluegrass roots on plants incubated at three temperatures (bars depict 95% confidence intervals).

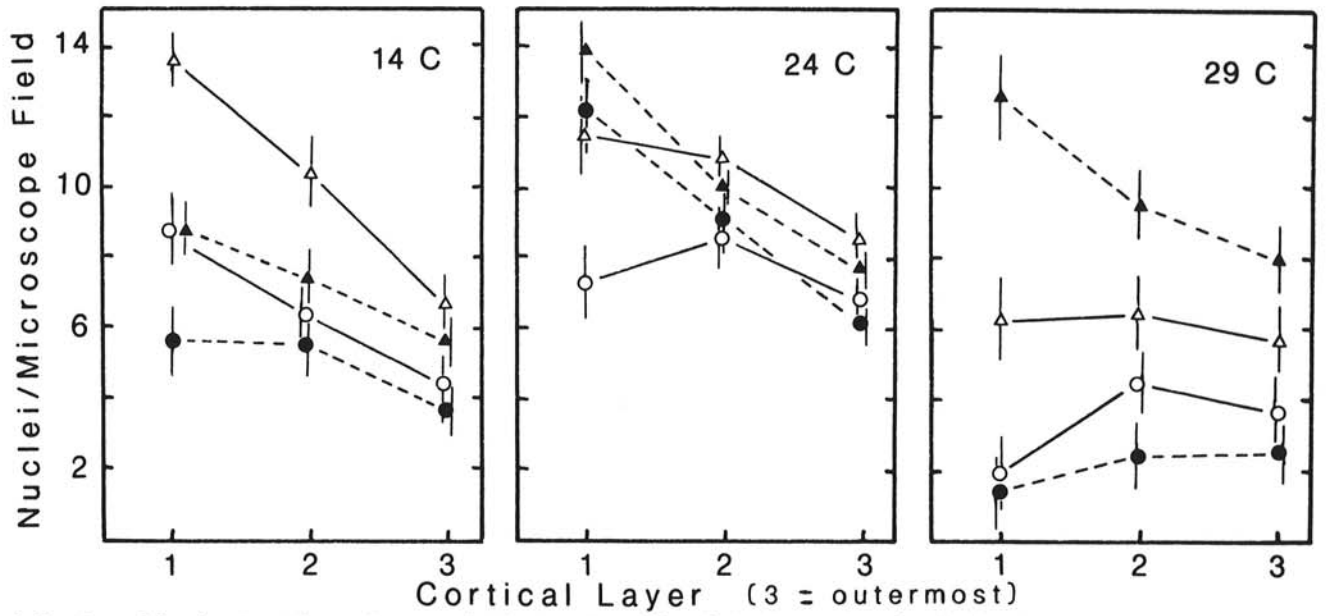

Fig. 2. Numbers of functional nuclei per microscope field in three layers of cortical cells near the apices (△▲) and crowns (○●) of 18-day-old Merion Kentucky bluegrass roots on plants incubated in shade (solid symbols) or full light (open symbols) at three temperatures (bars depict 95% confidence intervals).

Cultivars. Because the ultimate ability of the plant to resist colonization of the stele resides in the integrity of the endodermis and the cortical layer immediately outside the endodermis, counts of functional nuclei in this study were restricted to the innermost cortical layer. All treatment effects and their interactions significantly influenced the number of functional nuclei in the innermost cortical layer of roots in this experiment (Table 1). The cultivars Adelphi, Nassau, and Nugget showed pronounced differences in the number of functional nuclei in cortical cells at different light intensities (Fig. 4); Adelphi was intermediate in its response and Merion did not show a strong response to light intensity. The number of functional nuclei was reduced more at 29 C than at lower temperatures, but the actual response differed for each cultivar × temperature × light intensity interaction.

At 29 C under fully lighted conditions, the 25-day-old roots of all cultivars except Adelphi were devoid of nuclei in the innermost cortical layer. No temperature effect was observed on the nuclear status ot Adelphi roots when light was plentiful. Under shaded conditions, Nugget showed the best retention of nuclei at high temperature, Adelphi and Merion showed the poorest, and Nassau was intermediate.

Nuclei numbers in root cortices were compared with the magnitude of colonization of roots by *P. graminicola* and the foliar quality of seedlings by grouping all treatment variables together (i.e., cultivars, light intensities, and temperatures) for an examination of linear regression coefficients. Numbers of nuclei were inversely correlated with percentages of root area colonized by *P. graminicola* ($R^2 = -0.803$; $P = 0.005$) (Fig. 5) and directly correlated with foliar quality ($R^2 = 0.725$; $P = 0.05$) (data not shown). Foliar quality was also inversely correlated with percentages of root colonization ($R^2 = -0.697$; $P = 0.005$). The degree of root blackening was not significantly ($P = 0.05$) correlated with other measured parameters. Correlations and results were similar when the measurement parameters were compared only for plants incubated under full light in the growth chambers. For shaded plants, however, correlations were typically insignificant or weaker than those for their counterparts among the fully lighted plants.

DISCUSSION

The rate of nuclear autolysis in cells of Kentucky bluegrass root cortex tissue was responsive to interactions of the genetics, management, and environment of the plants. This natural, nonpathogenic process, called root cortical death, was strongly affected by the temperature and light intensity at which the plants were incubated, and the incubation conditions invoked different responses among the four cultivars studied. This appears to be the first report that temperature affects the rate of root cortical death in Gramineae and is the first report of this process in grasses cultured as turfs. Previous studies of this phenomenon in cereal grains have shown that the process is affected by light intensity (17)

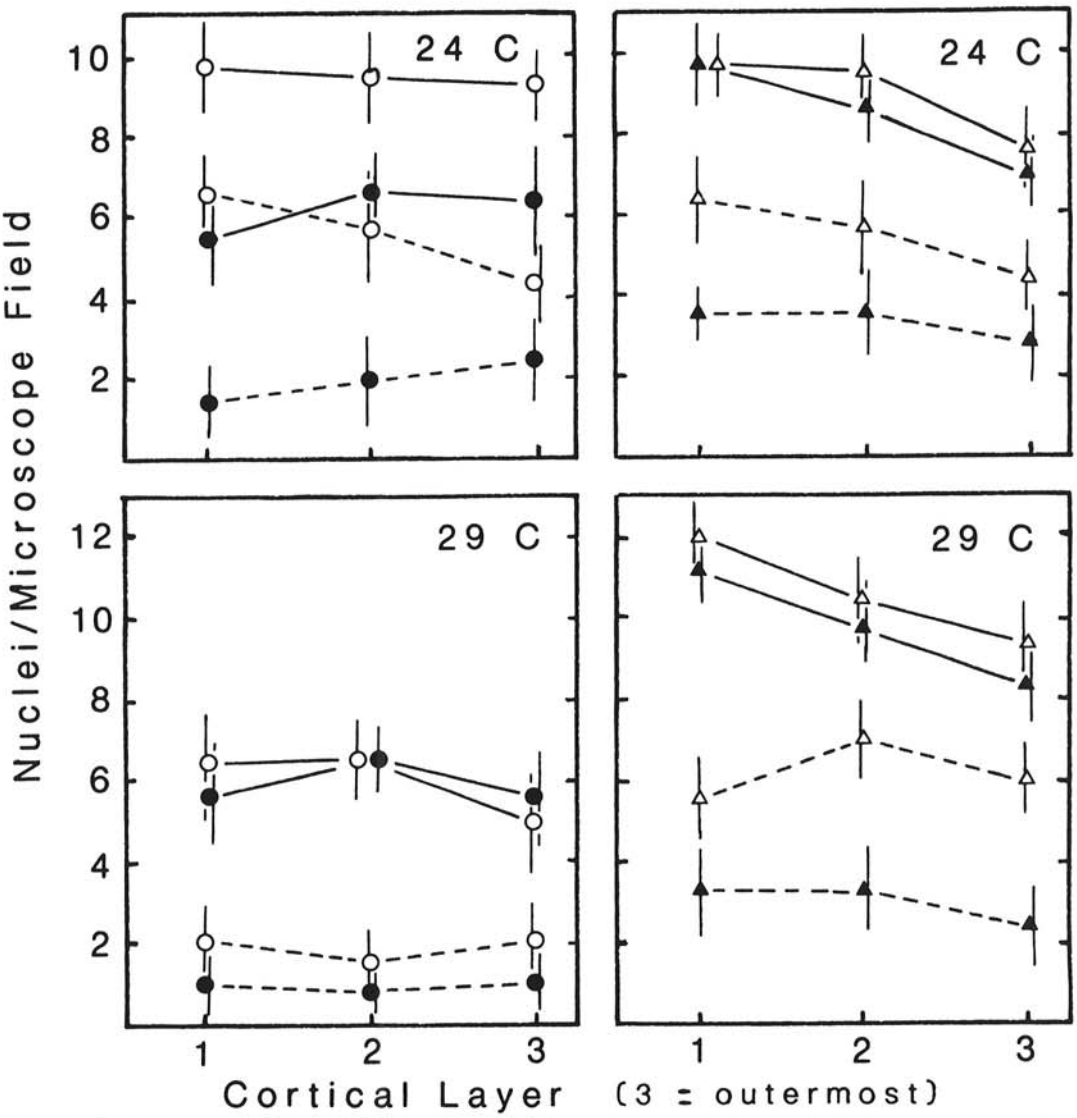

Fig. 3. Numbers of functional nuclei per microscope field in three layers of cortical cells near the apices (Δ ▲) and crowns (o ●) of 18-day-old Merion Kentucky bluegrass roots on plants in shade (solid symbols) or full light (open symbols) at 24 or 29 C and infected (dashed lines) or noninfected (solid lines) by *Phialophora graminicola*.

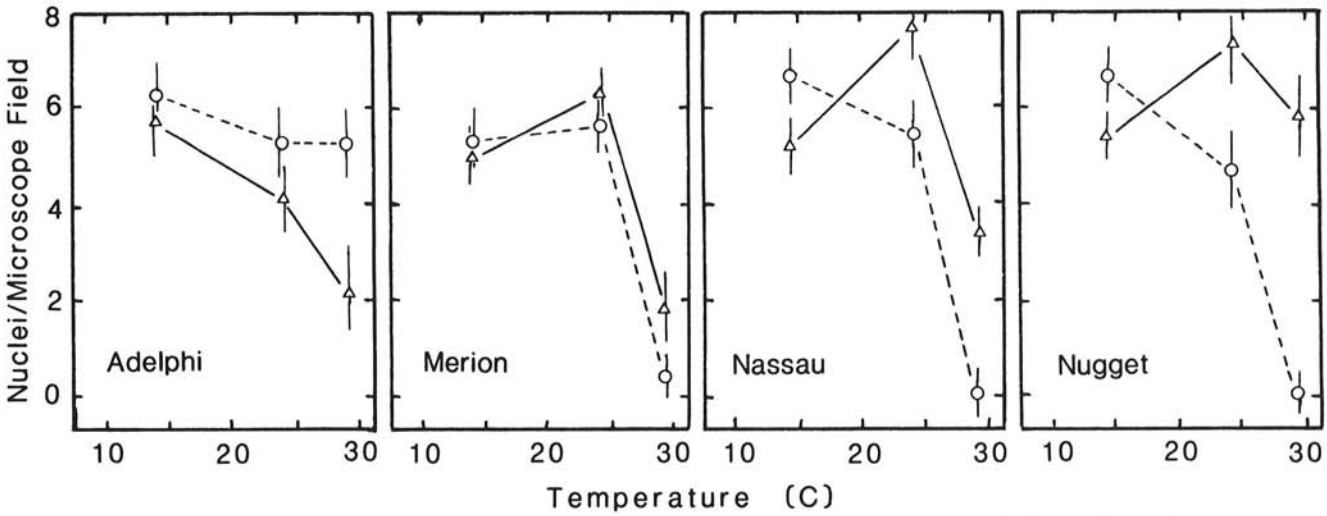

Fig. 4. Numbers of functional nuclei per microscope field in the innermost cortical layer of 25-day-old coronal roots for four cultivars of Kentucky bluegrass incubated in shaded (Δ) or fully lighted (o) positions in growth chambers at three temperatures.

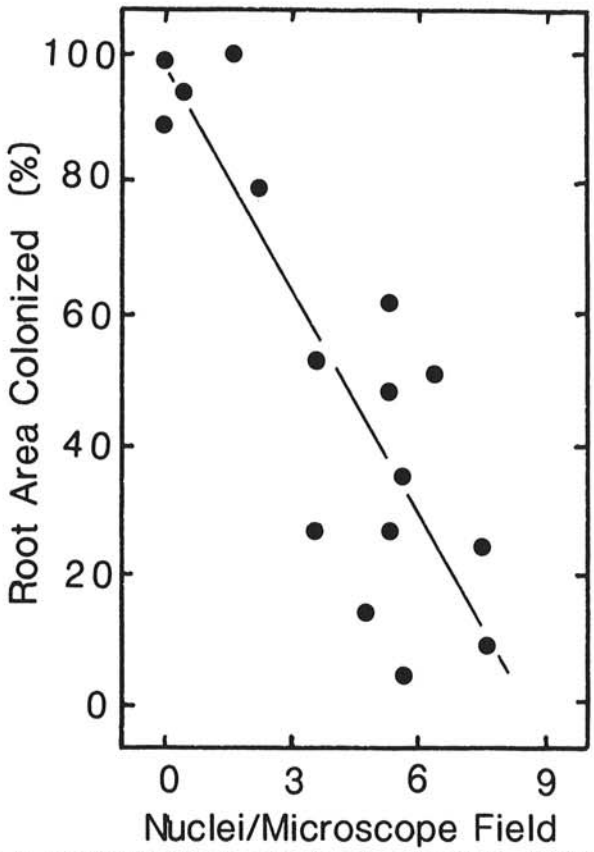

Fig. 5. Relationship between area of roots colonized by *Phialophora graminicola* and numbers of functional nuclei per microscope field in cortical cells of 25-day-old Kentucky bluegrass plants (cultivars Adelphi, Merion, Nassau, and Nugget) incubated in full light or shade at 24 and 29 C.

and that it varies among genera of Gramineae (9). Phytotoxins extracted from Kentucky bluegrass thatch, and possibly the mowing height of this grass, also affect the rate of root cortical death (23).

We found an inverse relationship between root cortical death and the ability of *P. graminicola* to colonize and cause necrosis of roots. Although we did not determine if root colonization by this fungus influenced the rate of root cortical death, previous investigations (6,8,12,15) suggest that this fungus in cereals does not affect the anucleation process but, rather, reflects that rate by its ability to colonize cells rapidly once the nucleus becomes nonstainable. It appears reasonable that *P. graminicola* also does not enhance the rate of root cortical death in bluegrass roots and that fungal colonization of the roots will, therefore, be affected by any factor that affects the rate of nuclear autolysis in roots. Before *P. graminicola* was recognized as a component of the patch diseases known as Fusarium blight, it was known that each cultivar's susceptibility to Fusarium blight became increased as the environmental and/or management conditions diverged from those considered optimal for the best performance of that cultivar (10,20). It would therefore be of interest to determine whether differences in rates of anucleation among cultivars of bluegrass seedlings, incubated under different environmental regimes, can be correlated with the field tolerance or genetic resistance of these cultivars to summer patch. If so, our results indicate that further evaluations of root cortical death in seedlings are warranted to determine if the process can be used as a quantitative indicator of plant stresses likely to predispose each cultivar to infection by root pathogens or as an early screening procedure to select plant genotypes with improved resistances to several important root-infecting plant pathogens.

Henry and Deacon (12) speculated that root cortical death may result from a decline in the amount of assimilate allocated to the root cortices as they age. Organic nutrients used to sustain young cortical cells may become redirected to more important areas of the root, such as the apex and laterals. Assuming this is true, one would expect an increase in root cortical death as environmental conditions become less favorable for translocation of photosynthates from the foliage to the roots. Our data provide additional support for Henry and Deacon's hypothesis.

The optimal soil temperature for Kentucky bluegrass root growth is about 10–18 C, and root growth is curtailed at about 25 C (3,16). The highest temperature used in this study is above that at which bluegrass roots can grow. Rates of anucleation for roots of fully lighted Merion Kentucky bluegrass were relatively uniform in the outer cortical layer of 18-day-old root segments at all temperatures and were sharply accelerated in the inner cortical layer at 29 C. If the supply of photosynthates to root cells is below the level necessary for maintenance of cell integrity, the first evidence of this stress should occur in the cortical cells nearest the vascular system, as was shown in this study. Further support for this concept occurred in the temperature × light intensity study. At 14 C, the rate of anucleation of cortical cells near the root apex was higher in shaded than in fully lighted plants. Shading had no effect on root cortical death at 24 C, and at 29 C the rate was much higher in fully lighted plants than in shaded plants. Lewis and Deacon (17) found that shading reduced the rate of root cortical death in seminal roots of wheat. Their experiment was conducted in the greenhouse at 22–25 C, with extremes of 20 and 32 C. Relative

balances among respiration rates in roots and shoots of plants do, therefore, appear to affect the rate of root cortical death.

The shading procedure used in our study was not indicative of the overall effects of shading in the field. In these growth chamber studies, the soil and lower plant canopy temperature was not reduced by shading (data not shown), as happens in the field. Under natural conditions, therefore, the effect of shading would be modified by a reduction of temperature on hot days. Our results suggest that the temperature-related effect on the rate of root anucleation may well be more important than a direct effect of reduced light intensity. More complex experiments are required to examine this hypothesis.

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