

AN ABSTRACT OF THE THESIS OF

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Title: Forecasting Pseudocercospora herpotrichoides Foot Rot
of Winter Wheat

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The use of fungicides for the control of foot rot of winter wheat, caused by Pseudocercospora herpotrichoides (Fron) Dei., requires a forecast of disease risk to optimize this management practice ecologically and economically. Foot rot occurs in both the mild, wet (100+ cm, ppt./year) annual cropped areas in western Oregon, and the drier (25-50 cm. ppt./year) summer-fallowed areas in eastern Oregon, that have colder winters and warmer summers. Adaptation to the wide range of conditions was examined to determine the need for considering ecotypic variation in a forecasting scheme. Although there were isolate differences, no in vitro growth patterns at 5-30°C on KCl or mannitol osmotically-amended media were indicative of ecotypic variation.

The forecasting data base, collected in 1979-80 and 1980-81, included climatological, geographic, agronomic and pathological factors for 39 commercial wheat fields from eastern and western Oregon. The best predictor of end-of-season disease severity from data collected by mid-season, when fungicide applications are made,

was the following multiple regression equation:

proportion severely infected tillers =

$$-1.08 + 0.04 \text{ RSF} + 0.20 \text{ SDEPTH} - 0.05 \text{ RSPACE}$$

where: RSF was a rain score from Sept. to Feb., which relates new infections with amount of daily precipitation; SDEPTH was seeding depth; and RSPACE was row spacing. The variables correspond with macroclimate of new infections (RSF) and microclimate important to disease development (seed date and row space). The model explained 74 percent of the variation in mean disease severity for eastern Oregon-grown Stephens wheat. Several diseases, especially take-all caused by Gaemannomyces graminis var. tritici, confounded foot rot assessments for western Oregon sites and rain score data exceeded values in the model; thus the model was not applicable to western Oregon sites.

Minimum yield losses, expected for particular levels of disease severity, were determined as a reference to severity forecasts. Significant ($P \leq .05$) yield losses occurred at intervals of approximately 15 percent (10-20) and followed the relationship:

$$\text{percentage yield loss} = -1.96 + 0.44 \text{ SF}$$

where: SF was the percentage of severely infected tillers. Analysis of individual-tiller yield components showed that under conditions of abundant moisture and no lodging, P. herpotrichoides reduced the number of kernels, per head, even with concurrent Septoria spp. head infections that affected both mean kernel weight and number of kernels per head.

Forecasting Pseudocercospora herpotrichoides
Foot Rot of Winter Wheat

by

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FORECASTING PSEUDOCERCOPORELLA HERPOTRICHOIDES

FOOT ROT OF WINTER WHEAT

CHAPTER 1

GENERAL LITERATURE REVIEW

The foundations of modern agriculture were laid some 9000 years ago when man began sowing seed that he had previously collected and saved. As agrarian societies increased in size, their survival depended on a bountiful harvest. Crop destruction by pests both seen and unseen became increasingly an object of concern. During these early days of agriculture, protection of crops was sought through the appeasement of the gods. Forecasts of natural disasters and disease outbreaks were even attempted based on astrological interpretations (Orlob, 1971). During the past two centuries, man has largely dispensed with the mystical, and has sought an improvement in agriculture through the biological sciences. Disease control is now based on scientific procedures, classified by Whetzel (1929) as exclusion, eradication, protection and immunization. The selection and integration of these disease-control procedures, with other agricultural practices and economics, is called disease management.

The process of developing a disease-management program (Apple, 1977) should include: identification of the problem, definition of the management unit, development of a management strategy, establishment of economic thresholds, and development of monitoring and predictive models. The present state of knowledge on the foot rot

disease of wheat (Triticum aestivum L.) with respect to these principles follows.

Problem Identification

Wheat is affected by a disease known as foot rot, eyespot, strawbreaker or Columbia Basin foot rot characterized by a necrosis of the basal portion of the plant. The causal agent of this disease, a fungus, is Pseudocercospora herpotrichoides (Fron) Deighton (syn. Cercospora herpotrichoides Fron). This organism was first described in France (Fron, 1912) from sporulating lesions on collapsed winter wheat stems. Fron was unable to complete Koch's postulates and prove causality because the fungus remained sterile in culture, causing confusion about the identity of the organism (Foex and Rosella, 1930). It was not until 1931 that Sprague, working in the Pacific Northwest (PNW), clearly established the causal nature of the disease.

P. herpotrichoides is a pathogen of certain wild and cultivated members of the Gramineae (Sprague, 1936; Cunningham, 1965). This relative selectivity has led many researchers to examine host specificity in some detail. Lange-de La Camp (1966) classified isolates into two main groups, named 'wheat' and 'rye' types, and five subgroups mainly on cultural characteristics. The two main groups did display some differential virulence to wheat and rye but not enough for formae specialis designation (Lange-de La Camp, 1966; Scott, Hollins and Muir, 1975; Scott and Hollins, 1977). Cunningham (1981) has recently discovered a third type which he isolated from Agropyron repens. Wheat or rye types cannot infect A. repens, while isolates from A. repens

can infect wheat but not rye. Nirenberg (1981), in examining the same question of isolate variability, concluded that there are actually two varieties of P. herpotrichoides, var. 'herpotrichoides' and var. 'acuformis', and also two new species P. anguioides and P. aestiva. This division is based mainly on conidial measurements.

Knowledge of the life cycle of P. herpotrichoides is still restricted to the asexual portion, but the lack of known sexual reproduction does not preclude genetic variability. Hybridization due to heterocaryosis (Davies and Jones, 1970) has been observed in this organism.

The basic disease cycle begins with previously infected stubble. Harvesting does not remove the basal portion of the plant, which if infected is the source of primary inoculum for subsequent crops (Sprague and Fellows, 1937). P. herpotrichoides is a poor saprophytic competitor for plant debris (Macer, 1961). Prior colonization of straw, through pathogenesis, prevents other organisms from invading the straw piece, and therefore reduces the value of a strong saprophytic competitive ability (Bruehl and Lai, 1966). The fungus can survive for at least two years on buried stubble (Peterson and Christensen, 1968), and possibly longer if the stubble remains on the surface (Byther, 1968).

Conidiophores, developing from the fungal tissue in previously infected stubble, produce conidia, the primary inoculum. Conidia are either splashed onto the host (Glynne, 1953; Bruehl and Nelson, 1964; Rowe and Powelson, 1973b) or moved with soil or soil water onto the infection court (Oort, 1936; Scheinpflug, 1964; McCoy, 1973). They

are produced in vivo optimally about 5-6°C (Jørgensen, 1964b; Drath and Rapilly, 1967). Sporulation in vitro also occurs at cool temperatures, -5 to 15°C when temperatures are fluctuating (Sprague and Fellows, 1934; Moritz and Bockmann, 1933; Glynne, 1953; Dickens, 1964; Diercks, 1966; Drath and Rapilly, 1967; Rowe and Powelson, 1973a), but the optimum appears to be about 9-10°C for constant temperature incubation (Chang and Tyler, 1964; Rowe and Powelson, 1973a; Ward and Friend, 1979). Peak periods of sporulation occur in both the autumn and spring (Hartz, 1969; McCoy, 1973; Van der Speck, 1975; Hollins and Scott, 1980). These periods correlate well with relative humidities greater than 80 percent when measured 2 m above the ground (Schrödter and Fehrmann, 1971a), resulting in moisture levels at or near saturation at the soil surface. In vitro studies show that excessive moisture may be inhibitory, but that greatest sporulation occurs when colonized plugs are kept in contact with water (Glynne, 1953; Drath and Rapilly, 1967).

Vegetative growth in vitro has been demonstrated to be relatively slow (Macer, 1961). Optimum hyphal extension occurs at about 19-23°C (Oort, 1936; Sprague, 1937; Ponchet, 1959; Dickens, 1964; Sekerkova, 1975), and optimum dry weight accumulation at 9°C (Dickens, 1964). Growth in vivo, measured as the number of leaf sheaths penetrated over time, paralleled in vitro growth which generally increased linearly from 6-18°C (Scott, 1971). Maximum and minimum temperatures for in vitro growth were found to be approximately 30°C and 0-3°C, respectively (Sprague, 1937; Dickens, 1964). The best moisture conditions for growth in vitro are between -4 to -10 bars when grown between 1-25°C, and

shifts to -8 to -22 bars when grown at 29°C (Bruehl and Manandhar, 1972). This shift corresponds with projected in vivo conditions of a gradually more negative water potential as the average ambient temperature increases through the growing season (Sprague, 1937; Cook and Papendick, 1972).

P. herpotrichoides infects coleoptiles and senescent leaf sheaths (Byther, 1968; Bateman and Taylor, 1976) within about 48 hours (Defosse, 1966; Bateman and Taylor, 1976) under cool, 0-15°C, moist conditions (Oort, 1936; Sprague, 1937; Lange-de La Camp, 1966; Defosse, 1966; Byther, 1968; Bojarczuk, 1970; Schrödter and Fehrmann, 1971b; Scott, 1971). Infections occur both above and belowground, and appear to be more frequent if the inoculum source is on the soil surface (Fromm and Feltz, 1976; Maenhout, 1977). This higher level of infection may be due to a release from biological competition (fungistasis) that occurs for below-ground inoculum sources (McCoy, 1973).

Losses from foot rot depend on the timing, incidence, and severity of infection. When infections are early and severe, P. herpotrichoides can kill the infected tillers directly (Scott and Hollins, 1974; Heyland and Fröhling, 1977) or reduce the number of tillers through increased winter kill. Stand reduction may be compensated for by increased tillering in spring or by increases in grain weight and numbers of kernels per ear (Ponchet, 1959; Lange-de La Camp, 1966; Scott and Hollins, 1974). Later or less severe infections can affect stem strength (Brück, Huth and Schlösser, 1980) and reduce grain number and 1000-grain-weight (Ponchet, 1959; Jørgensen, 1964a; Scott and Hollins, 1974; Clarkson, 1981). Loss in stem strength

can also cause plants to lodge, which has an additional indirect effect on grain yields (Scott and Hollins, 1974). The earlier lodging occurs, the more severe the effect (Glynne, 1944; Laude and Pauli, 1956; Weibel and Pendleton, 1964), presumably due to shading effects on photosynthate production needed for grain filling.

Epidemic development on susceptible hosts under favorable conditions is in a "simple-interest" (sensu Van der Plank, 1963) manner (Rowe and Powelson, 1973b). Theoretically, the outcome of a simple-interest epidemic can be altered dramatically by affecting the timing of the initial contact between host and pathogen. Early seeding, a desirable practice in the PNW because it provides wind- and water-erosion control and potentially higher yields, allows for early contact between host and pathogen. There is also an increase in the amount of senescent (susceptible) tissue available for infection at periods of peak sporulation (Powelson and Rhode, 1972) and increased canopy humidity (Bruehl, Nelson, Koehler and Vogel, 1968; Dickens, 1964), which commonly results in increased losses (Sprague, 1948; Dickens, 1964; Huber, 1967; Bruehl, et al., 1968; Bruehl, Peterson and Machtimes, 1974).

Management Unit Definition

The agroecosystem is an important concept necessary for a fundamental disease-management perspective. This concept magnifies the view of the agricultural system as an interacting group of components, thus helping to direct emphasis away from a narrow, pathogen-centered viewpoint, to a general, crop-centered viewpoint.

An agroecosystem, because of its low diversity, is similar in structure to a natural ecosystem at an early successional stage (Apple, 1977). Systems at this stage are in a dynamic state, creating many unfilled niches. Agroecosystems have a higher potential for change than natural systems because human inputs are maintaining them in a state of extreme biological imbalance. This maintenance is achieved through land preparation, weed control, fertilization, irrigation and pest control (Loomis, Williams and Halls, 1971). The imbalance is designed to channel all possible productivity to a desired crop. The result is that many more niches are vacant than in a natural system because of the drastic and quick effects of the management practices (Metcalf and Luckman, 1975). The potential for filling these vacancies is determined by the dispersal mechanisms of the organism (Apple, 1977). The dispersal mechanisms of a pest then determines the boundaries of the system to be managed with respect to that pest. P. herpotrichoides is a "soil-borne" pathogen with a maximum effective dispersal range between 1 and 5 m for the current crop season (Rowe and Powelson, 1973b; Magnus and Hansen, 1973). The maximum management boundaries for foot rot are therefore individual fields.

Management Strategies

Foot rot of wheat is a manageable disease. There are many available techniques that optimize epidemic reduction and general crop productivity. One such technique is the growing of resistant cultivars. In Europe, two sources of resistance are being pursued. The cultivar,

Capelle-Desprez, has a moderate level of resistance, manifested through smaller and fewer lesions than those on susceptible cultivars exposed to the same inoculum levels (Lupton and Macer, 1955). Capelle-Desprez is used as a parent line in the development of other commercial cultivars in Great Britain. Another parent line, VPM, having a higher level of resistance than Capelle-Desprez, was developed by Maia (1967), in France, from an interspecific cross (Aegilops ventricosa by Triticum persicum). There are no soft-white wheats "resistant" to P. herpotrichoides presently available for commercial use in the PNW. Some cultivars that are in production, though, resist lodging better than others, and some yield relatively well under moisture stress. These features confer some tolerance to the effects of the pathogen.

Chemical management of P. herpotrichoides is an available tool. Seed treatment with systemic fungicides initially delays the infection process, providing protection for several weeks (Schuhmann, 1968; Defosse, 1970; Benada, Vánová and Pešík, 1981). This protection does not affect any subsequent pathogen development, so that by the end of a disease-conducive season, no appreciable overall control is obtained (Bateman, 1977; Herman and Novotný, 1979). A single foliar application in early spring of systemic fungicides that produce methyl benzimidazole carbamate (MBC), on the other hand, is a very effective control measure (Powelson and Cook, 1969; Witchalls and Close, 1971; Powelson and Rhode, 1972; Bruehl and Cunfer, 1972; Huber and Mulanax, 1972; Fehrman, Reinecke and Weihofen, 1978; Sauer, Hampel, Locher and Mappes, 1980; Cook, 1980). Tolerance to the MBC fungicides has only

been found at background levels, $1/10^7$ - $1/10^9$ spores (Chidambaram and Bruehl, 1973; Fehrmann and Weihofen, 1978), even after three years of continuous fungicide use (Horstein and Fehrmann, 1980). Chlorocholine chloride has also been found to reduce yield losses mainly through its straw-strengthening properties, thereby reducing lodging due to the disease (Boland, 1969; Slope, Humphries and Etheridge, 1969; Witchalls and Hawke, 1970).

In the dryland regions of eastern Oregon, moisture is the major limiting factor for crop production; therefore the standard moisture-conservation practice is the use of a wheat-fallow-wheat crop sequence. Crop rotations, though, must be greater than one year out of cereals to be effective in reducing the amount of inoculum available for infection of a subsequent cereal crop (Glynne, 1965; Huber, 1967; Defosse and Rixhon, 1968; Debruck and Range, 1969; Fehrmann and Schrödter, 1971; Bockmann, 1976). Accordingly, summer fallow alone following wheat has little significant value in reduction of disease incidence (Huber, 1967; Defosse and Rixhon, 1968; Bruehl *et al.*, 1968). Stubble-mulch or no-till residue management, hypothesized to favor disease development by leaving residue at the surface, allowing inoculum dispersal, does not increase disease incidence (Brooks and Dawson, 1968; Cook and Waldher, 1977). Cook and Waldher postulated that the poorer initial plant growth in stubble-mulched plots produced a less favorable microclimate for fungal development, thus reducing disease incidence. Similarly, low seeding rates and distant row spacings (Glynne, 1942; Bawden, 1946; Sprague and Fellows, 1934; Bruehl *et al.*, 1968), as well as, low or no nitrogen fertilization (Heard, 1965; Dickens, 1964;

Cunningham, 1966) can result in lower disease incidence especially when used in combination with other disease reducing factors. Green manuring and the plowing in of a catch crop, grown between main rotation crops, can result in higher disease incidence, but may also slightly increase yields through the addition of nitrogen (Schulz, 1968; Debruck and Range, 1969; Obst, Graf and Rüppold, 1977; Lange-de La Camp and Naumann, 1978). The sanitation practice of burning the stubble is not efficient enough to significantly reduce inoculum levels, because much of the inoculum is at or below the soil surface (Sprague, 1937; Slope et al., 1969). However, plowing the debris in immediately after harvest can reduce disease incidence for the following season in continuous wheat cropping schemes (Lange-de La Camp, 1966). Because pathogen survival is known to be greater than one year on buried material (Cox and Cock, 1962; Lange-de La Camp, 1966; Cunningham, 1967), any subsequent tilling would bring up an inoculum source from which spores could be produced for dispersal and infection.

Establishment of Economic Thresholds

Economic losses due to P. herpotrichoides have been reported as high as 100 percent (Neururer, 1961). This estimate is not a reflection of the pathogen's ability to reduce grain yield to zero, but shows that yields can be reduced to the level at which harvesting would be uneconomical. Grain yield losses have been reported as high as 40 to 60 percent (Huber, 1967; Bruehl et al., 1968). These losses are attributable to severe infections producing lesions that nearly or completely girdle the stem (Ponchet, 1959; Jørgensen, 1964a; Defosse

and Rixhon, 1968; Bojarczuk, 1970; Scott and Hollins, 1974, 1978).

The implementation of a management scheme to reduce grain yield losses must increase the crop value greater than the cost of the particular practice or scheme (Apple, 1977). The resulting cost/benefit analysis requires knowledge of the yield loss relationship between host and pathogen, and also the cost of the management scheme on that relationship. Unfortunately, only elementary economic thresholds are presently available, because very few of the indirect costs are known.

Monitoring and Predictive Models

The implementation of a disease management scheme also requires a means to assess or to predict the disease intensity in order to determine whether or not the economic threshold will be attained. The only management practice that could be implemented easily after the crop had been sown is the use of a fungicide. Foliar fungicide applications against foot rot are made in late winter through early spring, at which time disease assessments are not reliable indicators that the economic threshold could be achieved (Scott and Hollins, 1978). Schrödter and Fehrmann (1973) developed a means of forecasting the disease levels by monitoring meteorological conditions. Their method involves calculation of an infection probability based on the frequency and duration of favorable temperature and relative humidity conditions. This method has proved difficult to utilize, since it best reflects conditions suitable for new infections and not the development of old infections in

severity (Polley and Clarkson, 1978). There are a few methods available that are easier to utilize, although their derivations are less data-based. The strength in the methods of Vez and Gindrat (1976), Bockmann and Effland (Lescar, 1977), and Lescar (Jenkins and Lescar, 1980) lies in the use of phytopathological principles in assessing the risk of disease development.

Much of the literature surveyed deals with the biology, etiology and cultural management of foot rot. There is still a great deal that needs to be done in the areas of management economics and forecasting. The following studies were conducted in order to develop a forecasting procedure for wheat growers in the PNW, and to provide a means of assessing those forecasts. Since wheat production in Oregon extends over a wide range of precipitation regimes, the forecasting system would need to take into consideration pathogen adaptation to those conditions. The first study, reported in Chapter 2, examines the possible existence of pathogen ecotypes. Chapter 3 deals with forecasting the final disease severity on an individual-field basis with information that can be collected by mid-season. Once a forecast is available, the most important criterion needed for making a management decision is the effect the disease can have on yield. Chapter 4 deals with yield-loss due to P. herpotrichoides, and includes information on yield-loss assessment with respect to concurring infections by Septoria spp.

CHAPTER 2

EVALUATION OF ECOTYPIC VARIATION IN
PSEUDOCERCOSPORELLA HERPOTRICHOIDES

INTRODUCTION

Ecotypic specialization in a pathogen could confound interpretation of results of disease-development studies that are necessary in the formulation of forecasting schemes. Pseudocercospora herpotrichoides (Fron) Dei., causal agent of eyespot or foot rot of winter wheat, occurs in two different regions in Oregon. The two regions are relatively well isolated from each other by the Cascade Mountains and differ particularly in total annual precipitation received. The Willamette Valley, on the west side of the Cascade Mountains, receives 100-125 cm of annual precipitation; and the dryland regions east of the Cascades receive 25-50 cm of precipitation per year (Anon., 1973). The two regions also differ with respect to mean monthly temperatures. Western Oregon has milder winters and cooler summers. The greatest differences in mean monthly temperatures between the meteorological stations in McMinnville (western Oregon) and Pendleton (eastern Oregon) occurred in January and July, 3.5 and 4.6°C, respectively (Anon., 1973).

P. herpotrichoides has been shown to have some degree of pathogenic specialization (Lange-de La Camp, 1966; Scott and Hollins, 1977; Cunningham, 1981), but never enough for a formae specialis designation. Nirenberg (1981) recently concluded that enough systematic morphological

differences exist for division of P. herpotrichoides into two new species and two varieties of P. herpotrichoides. This separation was based only on conidial measurements. Specialization in P. herpotrichoides is therefore prevalent in several forms, and may also be found with respect to distinct regional environmental conditions.

Bruehl and Manandhar (1972) had previously postulated the existence of a dryland ecotype of P. herpotrichoides. The results of their study on water relations of P. herpotrichoides did not support this hypothesis with respect to isolates collected across a range of dryland sites, 25-50 cm annual precipitation, in eastern Washington. No attempt was made to examine isolates from regions west of the Cascades because the pathogen was at that time considered to be of minor importance to that region (Bruehl, Nelson, Koehler and Vogel, 1968). It is quite probable, according to Dickens (1964), that P. herpotrichoides has been in western Oregon and Washington since at least 1919 as one of the organisms in a disease complex reported to cause a foot and root rot. Its increase in importance during recent years is most likely due to the increase in wheat in the crop rotations used in western Oregon and Washington.

The purpose of this study is to evaluate the possibility that ecotypic strains of P. herpotrichoides have developed in relation to the different amounts of regional annual precipitation and different temperatures in eastern and western Oregon. The most common means of obtaining information on fungal moisture requirements is to grow the organism at different osmotic potentials controlled by solutes.

Nutritional or toxic effects of the solutes are assumed to be minimal if different solutes at the same osmotic potentials produce the same effects on fungal growth (Griffin, 1977). Most researchers check for specific solute effects through graphical comparisons (Sommers, Harris, Dalton and Gardner, 1970; Bruehl and Manandhar, 1972; Cook, Papendick and Griffin, 1972); but Wilson and Griffin (1979) have shown that statistical differences still occur. The nutritional status, physiological age of the fungus, and temperature have also been shown to affect growth on osmotic-controlled media (Sommers et al., 1970; Bruehl and Manandhar, 1972; Cook and Christen, 1976). The general methodology, thus, has been to examine the growth trends on different solutes so that the relative effects can be ascertained (Wilson and Griffin, 1979; Luard and Griffin, 1981). This study examines the growth trends of P. herpotrichoides with respect to different solutes at different incubation temperatures, and also examines the growth trends on nutritionally different media.

MATERIALS AND METHODS

All studies were done on agar media adjusted to different osmotic potentials with reagent-grade salts or mannitol. The basal medium for examination of growth trends under high nutritional conditions was Difco potato-dextrose agar (PDA); in all others it was half-strength PDA ($\frac{1}{2}$ PDA) plus 0.75 percent Difco bacto-agar, to bring the agar content back up to 1.5 percent (w/v). All media were autoclaved at 121°C for 15 min. and dispensed with a syringe 10 ml per 60 x 15 mm petri plate (1007 Falcon; Becton, Dickinson

and Co., Cockeysville, MD 21030). Concentrations of amendments used to control osmotic potentials at the particular incubation temperatures were calculated for: mannitol, using the Van't Hoff relationship and assuming that the ionization constant for mannitol is one; KCl and NaCl, using the tables published by Wiebe (1971); and a 5:3:2 mixture of NaCl, KCl, and K_2SO_4 , using the calculations of Scott (1953) for NaCl, KCl, Na_2SO_4 . All the inoculum for the studies was grown at 20°C in the dark on primary plates of $\frac{1}{2}$ PDA. Primary culture incubation time varied from one to three weeks, but each study used isolates grown for the same length of time. Secondary plates, osmotically amended, were inoculated by cutting plugs from the leading edge of the primary cultures using a flame-sterilized cork borer (4 mm diam.) and were placed, mycelial side down, on the media. The inoculated secondary plates were incubated upside down in sealed plastic bags in the dark. Isolate designations used throughout this study (developed for record keeping purposes) consist of a letter indicating county of origin and several numerals. The first digit is a site designation code. The second digit indicates (0) parent isolates or (1-9) single-spored progeny, and the last 2 digit code following a slash is the year of isolation.

Specific Solute Effects

Two experiments were run to examine the reaction of several isolates of P. herpotrichoides to commonly used osmotic amendments. One experiment using a single isolate compared the amendments, mannitol and NaCl, at 0, -2, -5 and -10 bars for their effect on the radial

growth at a 10°C incubation. The other experiment compared KCl, NaCl and the mixture NaCl, KCl and K₂SO₄ at two amendment levels (-6.9 and -13.8 bars) for effect on radial growth of four isolates using a 25°C incubation. KCl is one of the most commonly used osmotic amendments, and is a calibrating solute in measurements of water potentials. Scott (1953) introduced the use of a 5:3:2 mixture of NaCl, KCl and Na₂SO₄ as an osmotic amendment to minimize any toxic effect of a specific solute. The colligative properties of equal molalities of K₂SO₄ and Na₂SO₄ are the same (Weast, 1971), so the calculations for the salt mixture (Scott, 1953) would produce the same osmotic levels in the modified form. The first experiment used five replicates, while the second used three.

Nutritional Effect

One experiment was designed to examine the effect of the basal media on results of experiments using osmotic potential-temperature treatment combinations. Two isolates used in the ecotype evaluation experiment were grown on PDA and ½PDA amended with KCl. The amendment range was -5 to -20 bars at 5-bar intervals. The incubation temperatures were 10, 15, 20 and 25°C; and the incubation period was one week. Four replications were used for all treatment combinations.

Ecotypic Evaluation

Fresh isolates, two from eastern Oregon sites that received 30 cm of annual precipitation, and two from western Oregon sites that received 105 cm of annual precipitation, were grown on media amended with KCl or

mannitol over a range of -5 to -20 bars at 5-bar intervals. The basal media was $\frac{1}{2}$ PDA, and the temperature range was 5 to 30°C at 5-°C intervals. Four replicates were used for each amendment type, temperature and osmotic potential combination. Two isolates, one from each region, were also grown at 25°C for one week on PDA amended with KCl at 10-bar intervals from 0 to -100 bars.

RESULTS AND DISCUSSION

Specific Solute Effects

The colony growth of P. herpotrichoides on mannitol-amended media was significantly higher ($P \leq 0.05$) than growth on NaCl-amended media, after two weeks. This difference occurred only at one level, -10 bars, of amendment. Since dextrose, in $\frac{1}{2}$ PDA, is readily available as a carbon source, and sugar alcohols are less available (Lilly and Barnett, 1951), mannitol acts as an osmoticum and not as a carbon source. The discrepancy in growth trends between mannitol and NaCl amendments at the high solute concentration is possibly due to a NaCl salt toxicity.

In order to further examine the possible toxicity of NaCl to P. herpotrichoides, four isolates were grown on media amended with KCl, NaCl or a modified Scott salt mixture, where K_2SO_4 was substituted for Na_2SO_4 to reduce the Na-ion concentration. There were differences in growth between isolates in general, so the results were divided by isolate for easier interpretation. In all but one case (U1-1/80) there was a significant salt level interaction (Table 1). This indicated that

the pattern of response, increased or decreased growth with increasing salt concentration, was salt-dependent. The mean response to NaCl as an amendment, over salt levels, was consistently lower than the response to KCl. The salt mixture was later measured with a vapor pressure osmometer (Wescor model 5100C) to be 1.5 bars higher than the KCl and NaCl solutions. Isolates U1-1/80 and U6-7/80 responded in the same way to KCl and to the salt mixture, even though there was this slight discrepancy in osmotic potentials. The difference in response by isolates P1-9/80 and Y1-9/80 to KCl and the salt mixture may be a result of P. herpotrichoides' sensitivity to the NaCl component of the salt mixture. The NaCl component of the salt mixture, at the high solute concentration, was only 0.021 molar less than NaCl concentration at the low solute level of NaCl alone. It is apparent from the two experiments that no two osmotic amendments would produce identical results.

Nutritional Effect

The growth on media containing higher levels of nutrients (PDA) at all levels of osmotic potential and temperature was greater than on $\frac{1}{2}$ PDA (Figure 1). One isolate in particular, P1-0/80, grew much better on PDA at all the osmotic potential-temperature combinations. The general pattern, decreasing growth with increasing osmotic potential and a shift in optimum osmotic potential at 25°C, was less pronounced but nevertheless occurred. The shift in optimum osmotic potential at 25°C for P1-0/80 was presumed to exist, but was not apparent because colony margins had reached the edge of the petri

plates prior to assessment after one week of incubation.

The actual values at which optimum growth occurred with respect to osmotic potentials were not the same. This corresponds with results obtained by Sommers et al. (1970) indicating that nutritional content of the media can alter the response to osmotic potentials. Although, type of osmotic amendment and nutritional content of the media produce different estimates of optimum values, the shape of the response curve is generally the same. The shape of the curve is therefore the first approximation of the fungal response to osmotic potentials.

Ecotypic Evaluation

KCl and mannitol were chosen for the regional-isolate-comparison study, because of KCl's common use and no apparent toxicity, and mannitol's different form and low nutritional value. The isolates Y2-0/80 and P1-0/80 were obtained from infected winter wheat grown commercially in western Oregon (Yamhill and Polk counties, respectively). The isolates U7-0/79 and U7-0/80 were obtained from commercially grown winter wheat in Umatilla county, in eastern Oregon. None of the isolates grew at 30°C. On KCl-amended media, after two weeks of incubation, growth of all the isolates was increasingly inhibited with decreasing osmotic potential when incubated at temperatures between 5-20°C (Figure 2). There were isolate differences at particular osmotic potential-temperature combinations for the 5-20°C temperature range, but the differences did not help distinguish between western and eastern Oregon isolates.

Incubation at 25°C produced a distinct shift in the optimum osmotic potential to a lower potential for all but the Y2-0/80 isolate (Figure 2). This shift in optimum at higher temperatures has been reported for P. herpotrichoides (Bruehl and Manandhar, 1972) and for other organisms as well (Manandhar and Bruehl, 1973; Cook and Christen, 1976). The greater shift in osmotic optimum at the high incubation temperature for the eastern Oregon isolates, as compared graphically to the western Oregon isolates, appears to indicate an ecotypic pattern of responses. Thus eastern Oregon isolates should have lower osmotic potential optimums at high temperatures than western Oregon isolates. The analysis of variance of colony growth for the KCl amendments did not substantiate this view. There were no significant ($P \leq 0.05$) isolate x osmotic potential and isolate x osmotic potential x temperature interactions. All main factors and the interactions of isolate x temperature, and osmotic potential x temperature were significant ($P \leq .025$). These interactions were interpreted to mean that all isolates responded similarly to osmotic potential, but that at least one isolate grew better than the others at some of the incubation temperatures. The shift in response to osmotic potentials at high incubation temperatures corresponds to the significant osmotic potential x temperature interaction. All isolates responded similarly to this interaction because the three-way interaction was not significant.

Mannitol as an osmotic-control agent did not produce identical results, as expected from the previous studies. However, the general trends of the growth response, e.g. shape of the response curves,

were similar. The trend was a decreasing growth response with decreasing osmotic potentials at 5, 10, 15 and 20°C incubations, and a shift in optimum osmotic potential at 25°C. The shift in response to osmotic potentials was greater for the western Oregon isolates, with mannitol as the osmotic control agent, than with KCl. The shift was not greater or more pronounced with mannitol for the eastern Oregon isolates. The difference between isolates, regardless of source, was even less apparent using mannitol as the osmotic amendment.

Two isolates, P1-0/80 and U1-0/80, were also grown on PDA amended at 10-bar increments to -100 bars (Figure 3). The faster-growing isolate, P1-0/80 from western Oregon, grew better regardless of the osmotic potential. No measurable growth occurred at -80 bars for U1-0/80, and at -100 bars for P1-0/80. The better growth and lower sensitivity to the salt at even these high salt concentrations for the western Oregon isolate were incompatible with the postulated ecotypic responses.

Although absolute growth responses varied considerably with any of the factors tested, the shape of the response curves with respect to osmotic potential and temperature was similar. The pattern of a high osmotic potential optimum followed by decreasing growth with decreasing osmotic potentials and a shift in osmotic potential optimum at 25°C is a first approximation of fungal response to osmotic potentials. Optimum values are only relative because of the differences with type of media and amendments. There were no in vitro growth differences attributable to P. herpotrichoides isolates obtained

from different temperature-precipitation regimes with respect to temperature of incubation and osmotic potential of the media. The high temperature shift in optimum osmotic potential to a lower (more negative) potential corresponds with in vivo conditions near the end of a growing season (Cook and Papendick, 1972) for both eastern and western Oregon. During late spring through early summer, as the wheat plant matures, rainfall in both regions diminishes and is accompanied by an increase in temperatures. The differences between regional macroclimatic conditions do not necessarily reflect the magnitude of the differences within the host tissue. These studies do not indicate that there are no ecotypes of P. herpotrichoides. The inability to differentiate between isolates based on the most obvious difference between the two regions suggests that regional adaptation does not need to be considered in the development of a forecasting scheme.

Table 1. The effect of KCl, NaCl and a 5:3:2 mixture of NaCl, KCl, and K₂SO₄ on in vitro growth of four isolates of Pseudo-cercospora herpotrichoides incubated at 25°C for one week in the dark.

Salt level (bars)	Colony diameter (mm) ^x			Anova ^y		
	Salt		Mix	Salt	Salt level	Salt x Salt level
KCl	NaCl					
Isolate: P1-9/80						
-6.9	16.833	14.167	18.500	.9982	.8878	.9998
-13.8	18.667	17.000	15.833			
Isolate: Y1-9/80						
-6.9	14.333	9.833	17.833	.9984	.9920	.999
-13.8	18.167	16.167	13.167			
Isolate: U1-1/80						
-6.9	21.667	19.833	12.000	.9992	.9999	.8134
-13.8	19.500	18.667	19.167			
Isolate: U6-7/80						
-6.9	20.667	18.167	20.833	.9999	.9996	.9949
-13.8	19.500	18.167	18.333			

^xMean colony diameters based on three replications.

^yProbability of significant F-test $P = (1-\alpha)$. P must be greater than .95 to be considered significant.

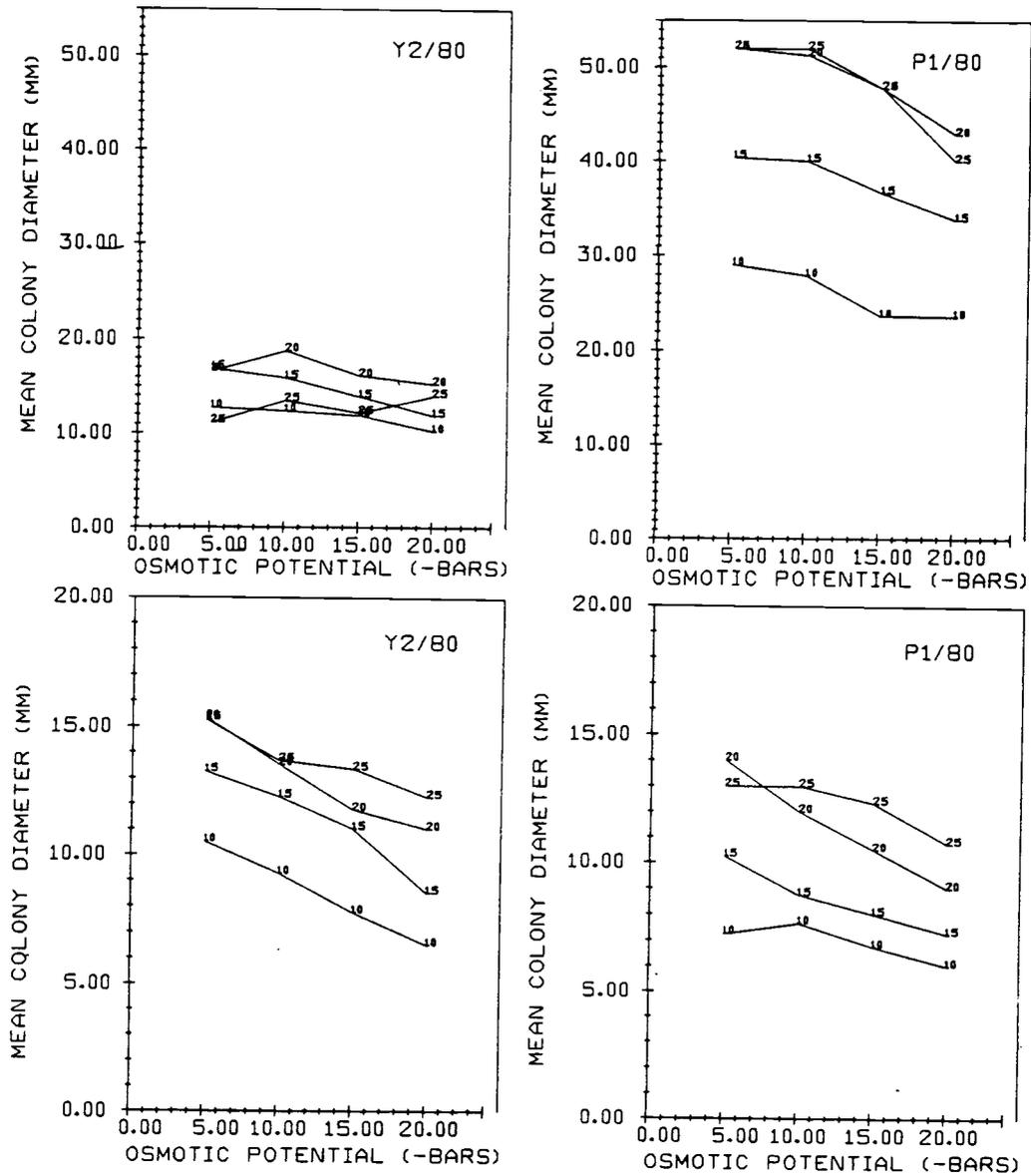


Figure 1. In vitro growth of two isolates of *P. herpotrichoides*, Y2-0/80 and P1-0/80. A-B. PDA amended with KCl, incubation time: one week. C-D. $\frac{1}{2}$ PDA amended with KCl, incubation time: one week. Numbers on individual lines indicate temperature of incubation.

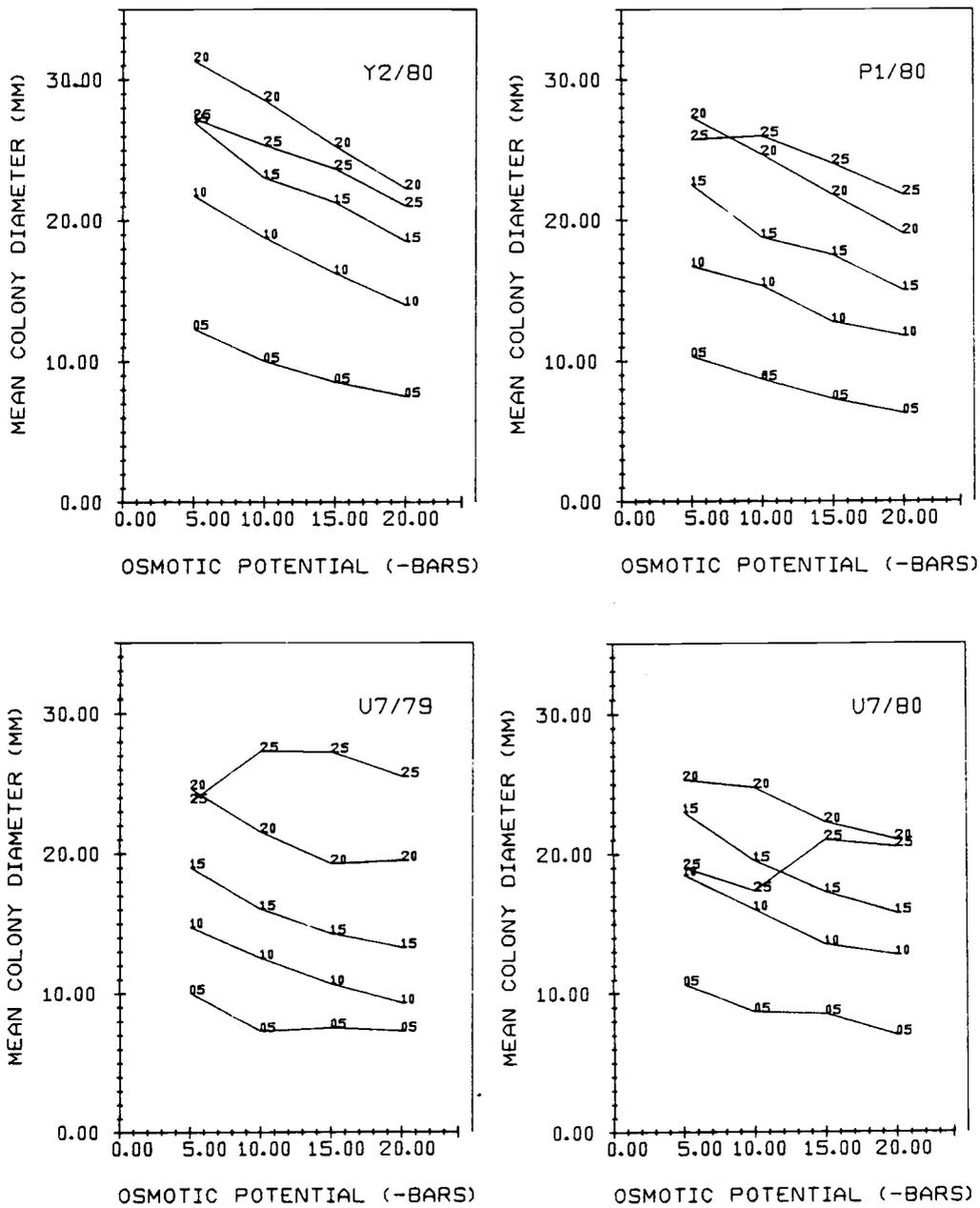


Figure 2. In vitro growth of four isolates of *P. herpotrichoides* on KCl-amended $\frac{1}{2}$ PDA after 2 weeks. Isolates Y2-0/80 and P1-0/80 were obtained from western Oregon, U7-0/79 and U7-0/80 from eastern Oregon. Numbers on individual lines indicate temperature of incubation.

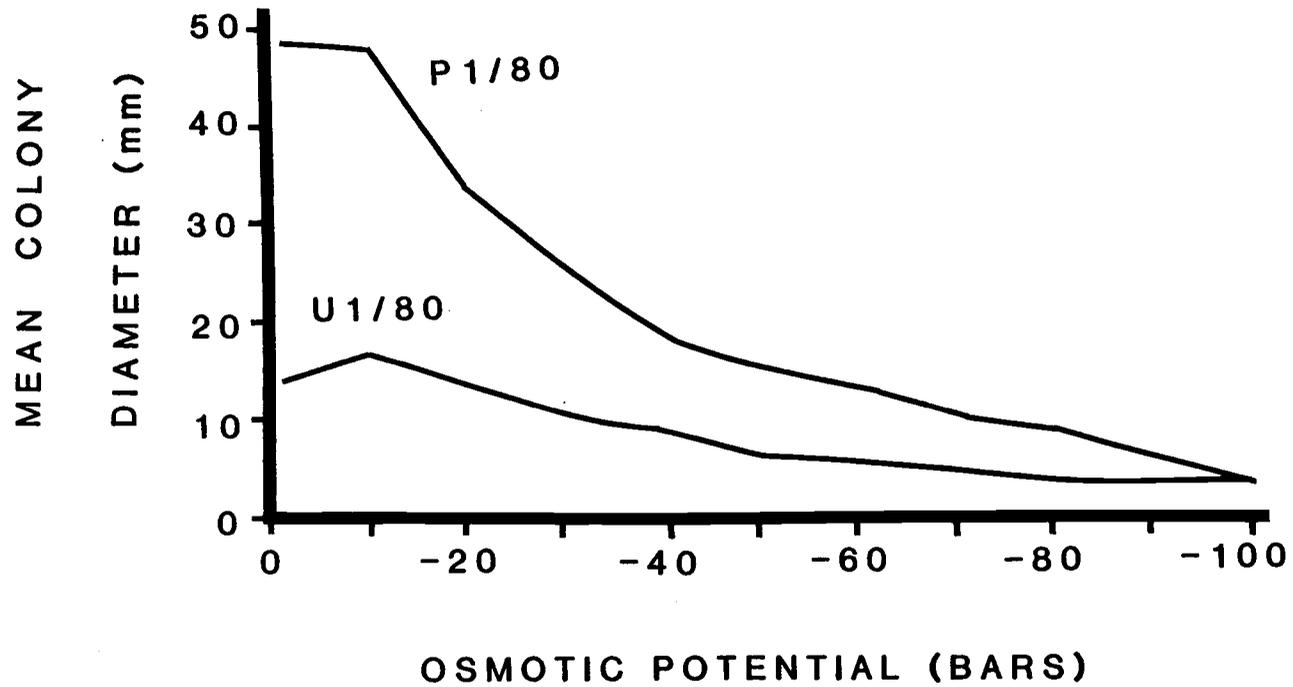


Figure 3. In vitro growth of two isolates, P1-0/80 and U1-0/80, of P. herpotrichoides at 25°C after one week of incubation on KCl-amended PDA (0 to -100 bars).

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CHAPTER 3

FORECASTING DISEASE SEVERITY OF PSEUDOCERCOSPORELLA
HERPOTRICHOIDES FOOT ROT OF WINTER WHEAT

INTRODUCTION

Pseudocercospora herpotrichoides (Fron) Deighton, causal agent of foot rot of winter wheat, is endemic to the winter wheat-growing regions of the Pacific Northwest (PNW). Depending on various climatic and agronomic factors, the severity of foot rot outbreaks varies considerably from year to year. Management practices like delayed seeding have been shown to reduce disease levels at the end of the season (Huber, 1967; Powelson and Rhode, 1972; Bruehl, Peterson and Machtimes, 1974). Unfortunately, early seeding is important in the stabilization of soils in the hilly wheat-producing regions against wind and water erosion. It also allows many cultivars to approach their yield potential more often (Bruehl, Nelson, Koehler and Vogel, 1968). During years with mild winters and prolonged cool-wet springs, unacceptable levels of disease may still occur even with the use of practices like delayed seeding. Management of foot rot may therefore require the use of fungicidal sprays.

Fungicides that produce methyl benzimidazole carbamate (MBC) are known to be effective in reducing P. herpotrichoides infections and to increase yields (Powelson and Cook, 1969; Defosse, 1970; Witchalls and Close, 1971; Powelson and Rhode, 1972; Bruehl and Cunfer, 1972). Recent research has shown that, although fungal resistance to these

fungicides can be found at background levels (Chidambaram and Bruehl, 1973; Fehrmann and Weihofen, 1978) after three years of continuous fungicide use, the fungicide-resistant population levels did not increase (Horstein and Fehrmann, 1980). Routine use, nevertheless, is not necessary and is uneconomical.

Economical use of these fungicides requires an assessment of the risk of severe disease for each particular field or portion of a field. Fungicide applications for the control of foot rot are made in late winter through early spring. Disease assessments during that time period are not only difficult (Amelung, Kaltschmidt, and Polak, 1978), but also are poor indicators of disease outcome and therefore of fungicide need (Scott and Hollins, 1978). In effect, a disease forecast is needed.

Several attempts have been made to produce foot rot forecasting systems. Schrödter and Fehrmann (1973) have devised a means of calculating a probability of new infections based on temperature and relative humidity alone. Their method was utilized for a few years in Germany by way of published forecasts from the German meteorological service (Obst, 1975; Frietag and Stingl, 1977). Vez and Gindrat (1976) in Switzerland, Bockmann and Effland in Germany (Lescar, 1977), and Lescar in France (Jenkins and Lescar, 1980) have all developed "score-sheet" forecasting systems. In general, factors used in these systems were selected, based on observations, experimentation and information from the literature. The relative importance of levels of the individual factors would be given an arbitrary score, e.g. 1-4, and then the sum of the scores for the factors would consti-

tute a forecast score. The success of these systems is difficult to assess because none of the authors have published verification data, and some of the factors are relative to local practices. This study was undertaken to develop a forecast of P. herpotrichoides applicable to the PNW, and to investigate improvements of the score-sheet weights through the use of multiple regression analysis.

MATERIALS AND METHODS

A data base was collected over two seasons (1979-80 and 1980-81) from 39 commercial winter wheat fields, representing a wide range of production areas (25-105 cm annual ppt.) in Oregon (Figure 4). Site selection was done in late winter through early spring with the aid of county extension agents and fieldmen for commercial agricultural chemical dealers. The selection was based on site disease history and visual inspection of plants for disease incidence. Sites determined by cooperators to require an MBC-generating fungicide (benomyl) for control of foot rot had three 3.6 x 6.1 m plastic tarps placed in the fields at the time of application, and were removed shortly after spraying. The tarped areas thus provided three replicated areas of untreated wheat, interspersed between three replications of treated wheat. Herbicides were later applied as required to the tarped areas, and were duplications of at least the class of herbicide used on the untarped areas. Supplementary sites were also chosen to include those with low or no disease history or incidence to complete the data base. These sites were sprayed with benomyl at 0.56 kg/ha in 187 l/ha of water using a bicycle wheel sprayer in three 3.6 x 6.1 m sections, thereby

maintaining the same experimental-unit size and number.

Disease incidence and growth stage of the plants were recorded as close to the time of fungicide application as possible. Background data with respect to disease history, agronomic practices, and edaphic characteristics of the site were obtained directly from the growers or by inspection (Appendix 1). Climatological data was obtained from the closest meteorological station (Appendix 2). Plant samples for the assessment of disease incidence and severity (proportion of tillers with at least half of the culm diameter necrotic) were obtained in June at approximately growth stage (GS) 75 (Zadoks, Chang and Konzak, 1974). Yields were determined in July at GS 92 by hand harvesting 2 rows 1.2 or 2.4 m long from the center of each experimental unit.

A FORTRAN program was written to reduce the daily climatological data to heat sums, rain scores, temperature scores and rain event sums. The heat sums were calculated with a 0 and 3°C base, using median temperature ($T_{max} + T_{min}/2$), and effective day and night temperatures sensu Went (Wang, 1963) (Appendix 3). These heat units were summed over the following time periods: monthly, and seeding date to spray date. Monthly temperature scores were calculated as a modification of Rowe and Powelson's (1973a) daily thermal sporulation coefficient. The modification was a change in the equivalent unit values (EUV) to a proportional scale (0-1) for ranges of temperatures (Appendix 3). Precipitation data from the meteorological stations was reduced to monthly and seed date to spray date sums of rain events. Rain events were defined as: standard (rain event = 1 if rain for the day was 0.01 in. or greater); Wang crop rainy day (Wang, 1963); and by dividing

all the parameters by a factor of two, a half-Wang crop-rainy day (Appendix 3). A rain score was based on an approximation (Appendix 3) of Ponchet's (1959) graph, relating intensity of rainfall with plant infection due to P. herpotrichoides.

Disease Incidence, Severity

Data were first examined with respect to the range in disease incidence and severity for the general effect of fungicide application. Separate analyses of variance for the two seasons were run with the factors, site and fungicide, as the "treatments" affecting disease severity and disease incidence. A least-significant-difference (LSD) value was calculated for the comparison of the within-site difference in disease between sprayed and unsprayed plots.

Predictive Models-Single Factors

Several of the Willamette Valley sites (any site code other than W or U) had severe take-all, caused by Gaeumannomyces graminis, var. tritici that confounded foot rot assessments. These and several other sites that had unique features were removed from the analyses described below because of their low representation in the data base. The following data analyses are for the cultivar Stephens grown in eastern Oregon, unless otherwise mentioned.

Correlation analysis was used to examine the relative linear correspondence of individual agronomic and environmental variables with disease severity. Variables that had extremely low correlations with disease severity were not included in the data subset used in

the regression analyses.

Predictive Models-Multiple Factors

Regression analysis was used to develop a predictive model for end-of-the-season disease severity, using variables that could be collected by mid-season (March 1). Stepwise regression in the Statistical Interactive Programming System (SIPS) was used. The SIPS stepwise procedure adds variables to the regression model that have the greatest contribution to the reduction of residual variance (Rowe and Brenne, 1981). The best model was selected by examining the significance of the regression parameters and the coefficient of determination (R^2) for the model.

RESULTS

Disease Incidence, Severity

The 1979-80 and 1980-81 growing seasons were generally conducive to disease development. There were no sites in the study without P. herpotrichoides-infected plants (Table 2), even though some sites were selected for low-disease history and no visual symptoms in spring. In general, 15 out of the 21 sites examined in the 1979-80 season had greater than 70 percent disease incidence, and nine had greater than 50 percent severely infected tillers by the end of the season. The 1980-81 season produced eight out of 17 sites with a disease incidence at the final assessment of 70 percent or greater, and nine sites with at least 50 percent of the tillers with severe lesions.

In all but two sites, U11 in 1979-80 and U13 in 1980-81, the mean

disease incidence and severity were lower for fungicide-sprayed plots than for the check plots. The tarps were inadvertently removed just prior to fungicide application for the U11 site (1979-80); so in that case there were no actual check plots. Therefore, there was only one case, regardless of disease history or incidence at midseason, where fungicide application was completely unsuccessful. However, the difference between sprayed and unsprayed plots was not statistically significant ($P > .05$) for some sites (Table 2). The difference in 1979-80 was significant for 14 sites with respect to disease incidence, and for 12 sites with respect to disease severity. In 1980-81, the differences were significant for 11 sites with respect to disease incidence, and for 10 sites for disease severity.

Predictive Models-Single Factors

Many individual factors that have been reported to be determinants of epidemic development either through controlled experiments (Sprague and Fellows, 1934; Bruehl et al., 1968), or through published score-sheet forecasts (Vez and Gindrat, 1976; Jenkins and Lescar, 1980) were poorly correlated with disease incidence, disease severity and yield loss (Table 3). Individually, without controlling the other factors, no one single factor could be used as a strong linear indication of final disease outcome. However, the variables that had the highest correlations were cumulative number of rain events, tillage method, and row spacing.

Two variables, both representing the number of rainy days between sowing and the time that fungicide was applied, had correlation coefficients (r) greater than 0.5. The highest correlations were with the Wang crop-rainy day variable. These crop-rainy day criteria ignore small amounts of rainfall (0.25 cm) unless they occur sequentially. The standard rainy day criteria, any day when rainfall is at least 0.025 cm, produced similar results, except for the correlation with disease severity. The sign for all these correlations was positive, indicating that an increase in rainy days increases disease.

The tillage score was a qualitative variable arranged with respect to the amount of soil disturbance each practice produces. There were only three categories: moldboard, disc and minimum plowing. There was only one site using minimum tillage, so that little can be interpreted from comparison to the other two categories. Means for the percentage disease incidence, percentage disease severity, and percentage yield loss, disregarding all other factors, for the moldboard and disc categories were: 60.2 and 13.8; 86.7 and 41.8; and 18.4 and 4.9, respectively. The lower values for disced plots, as compared to those obtained for moldboard plots, were similar to results obtained by Maenhout (1977).

Row spacing was the only other variable that had a correlation coefficient of at least 0.5. The negative correlations in this case indicated that as row spacings increased, disease incidence, disease severity and yield loss all decreased. All the other

correlations were below $r = 0.5$ (Table 3). Scatter diagrams did not indicate any strong curvilinear trends.

Predictive Models-Multiple Factors

Regression models that utilized variables mimicking those found in the published score-sheet systems had R^2 values of 0.50 when only 5 variables were included, and increased up to 0.74 when twelve variables were included. In the model with five variables, only one, standard rain event summed from seed date to spray date, had a significant regression parameter. Addition of any new variables improved the proportion of total variance accounted for, but also made all the regression parameters not significant.

The best model was obtained by using the stepwise procedure and limiting the number of variables in the model based on the significance of the regression parameters. The model was

$$\text{DIGT2} = -1.08 + 0.04 \text{ RSF} + 0.20 \text{ SDEPTH} - 0.05 \text{ RSPACE} \quad (1)$$

where: DIGT2 was proportion of severely infected tillers; RSF was daily rain score, based on Ponchet's work (1959), summed from September through February; SDEPTH was seeding depth in inches from the original soil surface; and RSPACE was row spacing in inches. The R^2 value for this model was 0.74, and the significance of the regression parameters were: $P = 0.0469$ for the constant; $P = 0.0012$ for RSF; $P = 0.0084$ for SDEPTH; and $P = 0.0231$ for RSPACE.

DISCUSSION

Disease Incidence, Severity

The objective for collecting these data was to acquire a data base on a wide range of foot rot disease outcomes in order to develop a forecasting scheme. The range in disease levels observed was satisfactory, but because of the conducive conditions during both seasons, outcomes of less than 10 percent disease incidence were not available. Therefore, disease forecasting based on these data would probably be "worst case" forecasts.

There are several possible reasons for the lack of difference in disease levels between some of the sprayed and unsprayed plots. One factor, the level of resolution, could have been improved by increasing the sample size. Another factor was plot location. The spatial distribution of the disease is not uniform, and it does not spread very far in a single season (Rowe and Powelson, 1973b). Variation in disease levels within the plot may therefore be high, since some replications may have more inoculum than others. Still another possible factor is the efficacy of the fungicide with respect to plant growth stage and date of application. Application when most of the plants are infected limits only the lesion development, not the number of tillers infected. Not all the sites were sprayed at the same growth stage or at the same level of infection.

Predictive Models-Single Factors

Disease dispersal has been shown to be highly dependent on rain

(Glynne, 1953; Bruehl and Nelson, 1964; Rowe and Powelson, 1973b) and rain intensity (Ponchet, 1959). The correlations for the rain event and row spacing variables thus have biologically supported interpretations. The narrower the row spacing, the more likely splash-dispersed spores would land on a susceptible host. Also, the resultant denser canopy would help to maintain a moist microclimate, which is conducive to infection and lesion development. The more frequent the rains, the greater are the numbers of effective dispersal events and the more persistent are the humid conditions that are necessary for infection and lesion development.

It is difficult to interpret the results of the disease comparisons with respect to the tillage practices because other factors varied between sites. No valid statistical comparison could be made. Yet there did not appear to be any particularly strong associations between a tillage method and a level of some other factors. Maenhout (1977), in a controlled series of experiments, observed lower disease incidence with disc plowing than with moldboard plowing. He concluded that the amount of surface inoculum was greater after moldboard plowing than after disc plowing. Cook and Waldher (1977) compared moldboard-plowed plots with stubble-mulched plots and found that foot rot was generally less severe in the stubble-mulched plots. These plots had a considerably greater amount of straw (potential inoculum) on the soil surface than the moldboard-plowed plots, but less disease. There is some disagreement in the literature on whether or not the pathogen survives longer on buried straw as opposed to surface straw (Macer, 1961; Byther, 1968). Cook and Waldher (1977) interpreted the stubble-management

effect on disease to be related to plant size and vigor in the fall because their stubble-mulched plants displayed poorer initial growth. The poor correlation between GSNOV, a score of the plant growth stage in fall, casts some doubt on that interpretation as well. It is possible that some other practice, in combination with the straw-management effect of the tillage practice, affects pathogen survival.

P. herpotrichoides produces a simple-interest type of epidemic (Rowe and Powelson, 1973b). Since outcome of simple-interest epidemics has a strong dependence on initial inoculum levels (Van der Planck, 1963), some measure of initial inoculum should, theoretically, be a good indicator of disease levels at the end of the season. This would especially be true if the rate of the epidemic does not vary a great deal. Reports of epidemic rates for P. herpotrichoides (rate of disease increase in units of $\ln(1/1-x)$, where x is the proportion of tillers infected) vary between 0.001 and 0.011 per unit per day (Rowe and Powelson, 1973b). Calculated rates from this study range from 0.002 to 0.037 per unit per day. The epidemics of P. herpotrichoides develop over long periods of time, e.g. October to June in the PNW; therefore the range of rates reported above would produce different disease levels at the end of a season with the same starting point. History of the disease, used in the site selection, was an indirect measure of initial inoculum based on grower estimates of previous crop damage. The correlation coefficients between disease history and disease incidence at the end of the season and disease severity were 0.176 and 0.327, respectively. Other measures of

initial inoculum would have little chance to improve the correlation because the rate of the epidemics differ for different sites, and thus different starting levels could result in the same end levels.

The poor correlation of disease incidence at mid-season with disease at the end of the season supports Scott and Hollins (1978). They have shown that disease incidence at mid-season was not a good indicator of fungicide need. Two reasons for this poor correlation are: disease assessments at mid-season are inaccurate due to latent infections; and disease development occurs over a long period of time, so that slight differences in epidemic rates would change the outcome for nearly identical sites.

An unexpected result was the poor correlation for seeding date with disease incidence and with disease severity. Several previous studies have shown that delayed seeding reduces disease severity (Bruehl et al., 1968; Powelson and Rhode, 1972). Late seeding affects the timing of the initial contact between susceptible host tissue and the pathogen. The duration of an epidemic is dependent on the length of optimal environmental condition, cool temperatures (0-15°C) and high humidity, that occur with respect to the appearance of susceptible tissue. Late seeding can therefore shorten the length of time available for epidemic development, and has been shown to be significant under normal (eastern Oregon, Washington) environmental conditions. The wet, cool springs and mild winters of the 1979-80 and 1980-81 seasons extended the time favorable for epidemic development, thus counter-

acting the effect of late seeding, The poor correlation for this well-documented management practice illustrates that none of the variables examined can indicate disease outcome over a wide range of cultural and environmental conditions by themselves.

Predictive Models-Multiple Factors

The best linear function that predicted disease severity at the end of the season, from data that could be collected by mid-season (March 1), was composed of agronomic variables and a transformed climatic variable. The rain score variable relates rain intensity to new infections. It was a good component of the predictor because both disease incidence and severity, at the end of the season, had a correlation coefficient of 0.91. It also indirectly characterized length of wet periods conducive to disease development. The other two variables, seeding depth and row spacing, were important in characterizing the microenvironment of the infection court.

The actual depth of seed placement was at most 1.5 in., but many growers in the dryland growing regions use deep-furrow drills to place the seed into moisture at the time of seeding. The furrow openers can place the seed up to four in. below the original soil surface and then cover the seed with 0.5 to 1.5 in. of soil. The furrows eventually erode due to wind and rain. This covering of the basal portion of the plant could bring inoculum to the culm tissue, protect the plant from splashed inoculum, or protect the infection court from desiccation after infection has occurred. Byther (1968) showed that tight crowned plants tended to have a majority of their

tillers infected; while plants with a wider spreading crown, at the same inoculum level, could be found with some healthy tillers. He also showed that infected leaf sheaths can become separated from the healthy adjoining tissue, stopping further penetration of the fungus into host tissue. Deeper seeding in both of these cases would maintain tighter crowns and prevent senescing sheaths from sloughing away from healthy tissue.

Row spacing has been previously implicated as a factor in disease severity development (Sprague and Fellows, 1934), in particular in years when growing seasons are not very favorable to disease development. The interpretation thus was that wider spacings would produce subcanopy conditions which would be less favorable for disease development. The weather during the two seasons of this study was favorable, even in the late spring, for lesion development. The wider row spacings could reduce the probability of successful hits and thus affect disease incidence and severity directly. Wider row spacing and deep-furrow drilling are techniques used by growers in the lower-rainfall areas. The two variables may be in the model simply because they indirectly classify the climatic conditions of the site.

Prediction of disease severity for the Willamette Valley could not be done using equation 1. The difficulty is not due to any differences in the pathogen (Chapter 2), but is a result of the range in the data used in model formulation. The regression equation overestimates disease severity if an attempt is made to use it for the Willamette Valley. The primary reason for the overestimation

is the range of the rain-score variable. Willamette Valley sites receive much more rainfall during the fall through early spring growing period. These data were out of range for the model which illustrates the danger of extrapolation, as well as the non-cause-and-effect estimation of the relationship between dependent and independent variables in a regression model. A larger data base that would have replicated factor combinations would allow for selection of variables sensitive to disease-severity estimation for both regions. Another approach that could help solve the problem of variable selection for the development of a widely applicable predictor would be to have controlled multi-factored experiments in both regions.

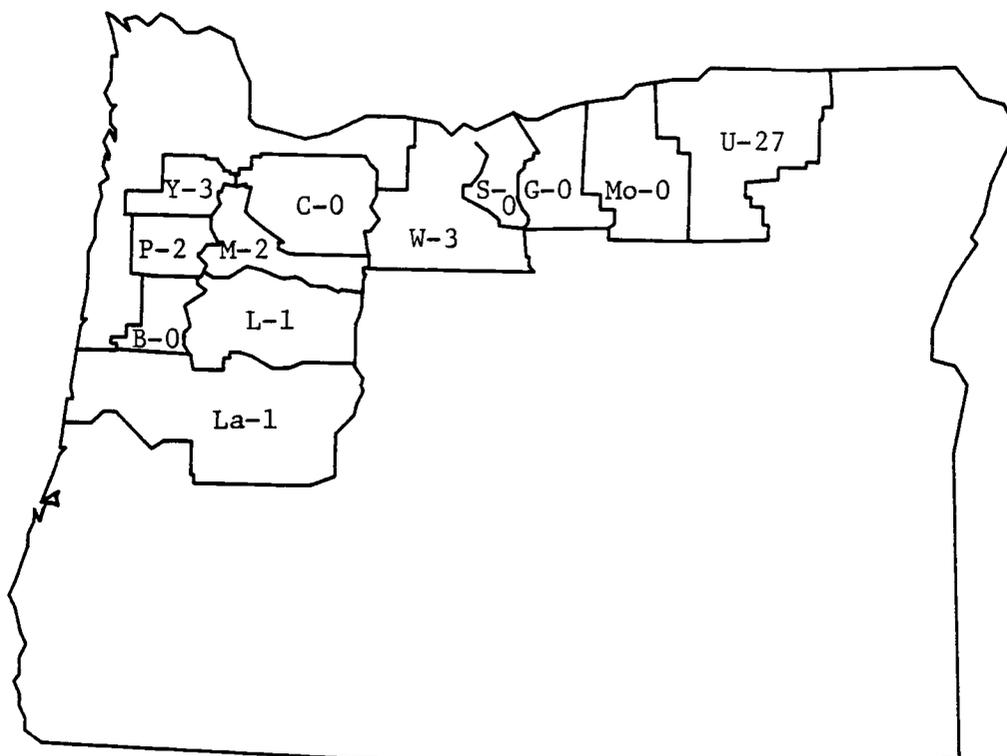


Figure 4. Counties of the major winter wheat-producing areas of Oregon. County code followed by a number indicates number of sites included in the study over two years. B = Benton, C = Clackamas, G = Gilliam, La = Lane, L = Linn, M = Morrow, P = Polk, S = Sherman, U = Umatilla, W = Wasco, Y = Yamhill.

Table 2. Mean incidence and severity of foot rot for benomyl-sprayed and unsprayed plots examined during the 1979-80 and 1980-81 growing seasons.

Site ^a	1979-80				Site	1980-81			
	Incidence ^b		Severity ^c			Incidence		Severity	
	Spray	Check	Spray	Check		Spray	Check	Spray	Check
M2	15.4	34.9	4.3	23.1	U9	17.5	58.0	10.4	41.6
P1 s	53.7	77.0	13.5	26.7	U7	25.7	97.5	17.7	95.1
U10	95.4	98.7	67.3	84.5	U4	12.0	17.1	5.1	7.9
U11	77.5	78.7	30.4	30.6	U11	17.5	53.9	7.2	24.2
U12	48.9	88.2	22.4	53.2	U1	8.4	30.1	3.8	21.4
U13	17.5	74.8	4.7	32.1	U10	5.8	11.8	2.4	6.5
U14	33.4	41.8	9.5	16.1	U6	23.3	87.7	13.0	75.5
U1	52.8	88.0	21.7	38.7	U5	49.7	91.4	27.1	82.2
U2	35.4	87.7	15.0	59.0	U8	22.4	74.1	8.5	58.0
U3	18.7	66.4	8.3	28.1	U3	1.3	11.3	0.6	6.6
U4	47.3	89.0	32.1	74.6	U2	17.5	50.5	11.1	15.0
U5	50.3	94.9	15.2	80.2	U13	19.8	17.4	8.2	7.0
U6	44.6	97.8	18.4	68.2	P1	15.5	98.6	10.0	75.9
U7	54.7	90.7	24.9	61.9	La1	21.0	57.3	11.0	52.3
U8	52.8	83.6	34.7	54.2	L1	42.2	79.7	24.3	73.7
U9	22.4	33.7	5.3	16.7	Y1	85.9	99.6	57.7	90.5
W1 s	37.1	44.8	10.7	1.37	M1	58.4	89.4	49.4	81.8
W2 s	4.7	18.4	0.6	3.6					
W3 s	38.1	71.1	13.1	27.9					
Y1	47.5	88.9	23.9	37.3					
Y2	49.6	89.3	18.9	63.7					
LSD. (.05) ^d	19.8		16.3			28.1		22.6	

^aSite codes followed by (s) indicate supplementary sites that were determined by cooperators not to require fungicide application.

^bMean percentage of disease incidence based on 100 tillers per replicate, up to three replications per site.

^cMean percentage of disease severity (tillers with at least half culm diameter necrotic) based on 100 tillers per replicate, up to three replications per site.

^dDifference required between sprayed and unsprayed plots within a site for significance at $P = 0.05$.

Table 3. Correlation coefficients for foot rot incidence, severity and resultant yield loss correlated with various factors using eastern Oregon data only.

Factor	Disease		Yield Loss ^b	Factor Description
	Severity ^a	Incidence		
SDEPTH	-.342	-.400	-.385	Seeding depth from original soil surface
TILLAGE	-.616	.546	-.432	Moldboard, disc or low till
SDATE	.228	.376	.446	Seeding date, continuous numbering from Sept. 1
SRATE	.396	.355	.434	Seeding rate (lbs/acre)
RSPACE	-.531	-.597	-.431	Row spacing in inches
HSTROT	.327	.176	.198	Foot rot history
DIMID	.394	.323	-.007	Disease incidence in March
GSNOV	-.189	-.294	-.277	Zadoks <u>et al.</u> growth stage mid November
HTSDTSP	-.208	-.421	-.472	Heat sum median temp seed date to spray date
HTSDSPED	-.179	-.362	-.428	Heat sum effective day temp seed to spray date
HTSDSPEN	-.239	-.451	-.491	Heat sum effective nite temp seed to spray date
RO1SDTSP	.556	.673	.586	Sum rain days \geq 0.1 in. seed date to spray date
WRSDTSP	.618	.676	.586	Wang rainy days sum seed date to spray date
WR2SDTSP	.418	.506	.557	Wang rainy days/2 sum seed date to spray date

^aPercentage of tillers with severe lesions (greater than half culm diameter necrotic).

^bYield loss relative to spray yield $[1 - (\text{check yield}/\text{spray yield}) \times 100]$.

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CHAPTER 4

YIELD LOSS IN WINTER WHEAT CAUSED BY
PSEUDOCERCOSPORELLA HERPOTRICHOIDES

INTRODUCTION

Forecasts of diseases with outputs of expected disease incidence or severity are generally only meaningful to plant pathologists familiar with the particular pathosystem. The grower needs a frame of reference in order to assess the meaning and significance of disease forecasts. That frame of reference is the relationship between disease and yield loss.

Yield losses due to Pseudocercospora herpotrichoides (Fron) Dei., causal agent of foot rot of wheat, occur when the lesion nearly or completely girdles the culm of a susceptible host (Ponchet, 1959; Jørgensen, 1964; Scott and Hollins, 1974). Additional losses occur if lodging due to weakened, infected stems is prevalent during grainfill (Scott and Hollins, 1974). Several yield loss relationships have been developed for foot rot (Scott and Hollins, 1978; Fehrmann, Reinecke and Weihofen, 1978), but these relationships were based on losses determined relative to fungicide-treated plot yields. Clarkson (1981), using a single shoots and individually threshed heads, could demonstrate losses at moderate disease severity levels, and developed a disease-yield relationship with losses calculated relative to yields of uninfected tillers. However, he found it difficult to relate these data back to large-scale field situations.

In the field, the cultivated wheat plant is rarely grown in the absence of disease producing pathogens. In fact, several different pathogens commonly infect the same host plant. Thus, when evaluating any particular host x pathogen response the impact of other diseases must be taken into consideration. Recently, there have been some studies with winter wheat which examined the effect of prior inoculation with Gaeumannomyces graminis (Sacc.) Arx and Olivier var. tritici Walker, causal agent of take-all, or P. herpotrichoides on Septoria nodorum (Berk.) Berk. infections (Jones and Jenkins, 1978; Jenkins and Jones, 1980) and on Puccinia recondita Rob. ex Desm. f. sp. tritici infections (Grigor'ev, 1980). Individually, S. nodorum, S. tritici and P. herpotrichoides infections have been demonstrated to reduce plot yields and 1000-kernel weights (Eyal, 1972; Sharp, Brönnimann and McNeal, 1972; Scott and Hollins, 1974). Jones and Jenkins (1978) concluded that, although there was an increase in S. nodorum incidence by pre-inoculating the plants with P. herpotrichoides, there was no significant yield loss interaction. They were also unable to demonstrate any effect of P. herpotrichoides alone on yield.

Infection of winter wheat by Septoria tritici Rob. ex. Desm. is a common occurrence in western Oregon. It is rarely a pathogen of any economic importance because the rains critical for severe epidemic development (Shaner and Finney, 1976) generally subside by late spring, limiting infections to the lower leaves of the plant, which have little effect on yield. Occasionally, as in the 1980-81 growing season, the rains continued well into the grainfill period causing severe infections

of the flag leaves and glumes. Isolations showed that both S. nodorum and S. tritici were present and percentage of head attacked was over 70 percent (unpublished).

The purpose of this study was to develop a frame of reference for a foot rot forecasting system (Chapter 3). Because of the opportunity to examine yield-loss interaction, P. herpotrichoides yield-loss assessments were made relevant for western Oregon growers by examining its effect on yield and yield components on a single-tiller basis when concurrent head infections due to Septoria spp. occurred. A method to relate single-tiller assessments to larger-scale plot yields using a montecarlo procedure is proposed. A yield-loss threshold, proportion of P. herpotrichoides severely infected tillers required for a significant loss, and yield-loss model are developed using the montecarlo procedure. Yield-loss model predictions are verified by comparison to yields determined on a plot-scale.

MATERIALS AND METHODS

Stephens, a soft white winter wheat cultivar, was sown at the Oregon State University North Willamette Experiment Station near Aurora on October 23, 1980. The ground had been previously summer fallowed after a crop of blackberries. The seeding rate was 67 kg/ha with rows 30 cm apart. The plot area, 15 x 60 m, was divided into 140 2 x 3 m plots. The herbicide, diuron (3-(3,4-dichlorophenyl)-1,1-dimethyl-urea) was applied for weed control; and the plots were

fertilized in October with 807 kg/ha of 10-20-20-7, and in March with 373 kg/ha of $(\text{NH}_4)_2\text{SO}_4$.

P. herpotrichoides colonized oat inoculum was prepared following the procedure of Bruehl and Nelson (1964) using four different isolates. The four sets of air-dried inoculum were mixed together and broadcast at a rate of 25 kg/ha, when the plants were in the 2-3 leaf stage, growth stage (GS) 12 (Zadoks, Chang and Konzak, 1974), on December 18. The entire plot area was infected with Septoria spp. due to naturally occurring inoculum. Half of the plot area was sprayed on March 12 with benomyl (1-(butylcarbamoyl)-2-benzimidazole carbamate) at a rate of 0.56 kg in 187 l water per hectare for the control of foot rot.

Single Tiller Yield Loss Assessment, Disease Interactions

Disease assessments for the single-tiller assay were made on July 29, when the plants were ripe, GS 92. At that time, approximately 100 plants with their associated tillers were dug up from unsprayed inoculated and uninoculated areas after enclosing the individual heads in bags to avoid loss of grain. The culms were assessed for severity of foot rot by cutting through the center of the lesioned area and rating the necrosis on a 0-5 scale (Table 4). The heads were assessed for area discolored due to Septoria spp., also on a 0-5 scale (Table 4). The length of the heads from basal to terminal spikelet was measured, and then individually threshed. The grain from the individual heads was weighed, counted and mean kernel weight determined. A total of 279 heads were assessed in

this way. Preliminary analysis indicated that several of the 36 possible combinations of severity of infection by P. herpotrichoides and Septoria spp. were not represented. The disease classifications were then consolidated into 3 point scales (0-1, 2-3 and 4-5), which also made both scales center-weighted like the many available variations of the Horsfall-Barratt scale (1945). The single-tiller data was analyzed using a Bonferroni multiple comparisons procedure because of the unequal sample sizes in the data matrix (Neter and Wasserman, 1974).

Foot Rot Yield Loss Threshold, Model

A major obstacle in developing a yield loss model is obtaining data that provides a wide range of replicated classes of disease severity (e.g. 5 plots with 10 percent severely infected tillers, 5 plots with 20 percent, etc.) without introducing other sources of variation. The initial estimation of a yield loss relationship can be achieved through a montecarlo simulation of replicated classes of disease severity. Different combinations of slight and severely infected tillers with P. herpotrichoides were generated by a monte-carlo procedure (Rowe and Brenne, 1981) using the results of the single-tiller assay. The parameters of the simulated populations were the means and standard deviations of the number of kernels per head for the low Septoria spp. infection category and the low, medium and high foot rot infection categories. The generated combinations simulated "field"-collected data for mean number of kernels/100 tillers/replication. There were five replications, and the

combinations had 0, 10, 20, 50, 80 and 90 tillers with severe foot rot; the remaining tillers out of 100 were uninfected. A yield loss threshold, lowest proportion of infected tillers that will cause a significant ($P \leq .05$) yield loss was evaluated using an analysis of variance of the generated "field" data and a Duncan's multiple range test. A regression equation (yield loss model) relating percentage of tillers with severe foot rot to percentage yield loss was then generated. Yield loss was calculated relative to the mean number of kernels per head in the low infection category of the original data set.

Single Tiller-Plot Scale Comparisons

Foot rot disease assessments were made at GS 75 on June 10. One hundred tillers from ten randomly selected plots per sprayed and unsprayed sections, both inoculated and uninoculated, were assessed for depth of lesion penetration as described for the single-tiller assay. Harvest samples from another ten randomly selected plots per treatment combination were taken on July 29. Harvesting was done by hand, scything two 1.4 m row lengths and then threshing with a Vogel thresher. Total grain weight and 250-kernel weights were recorded. The remaining plots were used in a study of disease progress not reported here. The generated data was also compared to actual plot yields and disease severity determined at the June sampling period.

RESULTS AND DISCUSSION

Single Tiller Yield Loss Assessments, Disease Interactions

Sampling along an inoculum gradient, that is from an inoculated area to an uninoculated area, produced a fairly uniform number of observations for all three classes of foot rot severity (Table 5). Septoria spp. head infections were due to natural inoculum, and therefore there were more observations in the slight and moderate infection categories than in the severe category (Table 5). The correlation between the severity of foot rot and severity of Septoria spp. infections was very low ($r = -0.08$), indicating that the severity of Septoria spp. head attack was not a function of prior infection with P. herpotrichoides. Foot rot may have predisposed the plants to Septoria spp. and caused an increase in the incidence of head infections (Jones and Jenkins, 1978), but the severity of Septoria spp. head infections was influenced to a much greater extent by the duration of the late spring rains that occurred that season (Shaner and Finney, 1976).

Total grain weight per head, and two yield components, mean-kernel weight per head and number of kernels per head, were examined. Mean-kernel weight is a quality index indicative of the effect the pathogens may have on the grainfill process. It is related to 1000-kernel weight by a factor of 10^3 . The number of kernels per head is a quantity index indicative of the pathogens effect on grain set or floret development. The two yield components and total yield were affected significantly by Septoria spp. head infections (Table 6).

P. herpotrichoides foot rot affected the total yield and the quantity component, number of kernels per head, but not mean kernel weight.

P. herpotrichoides and Septoria spp. interacted significantly with respect to their effects on total yield and number of kernels per head (Table 3).

A detailed examination of the effect of the pathogens on the quality index, mean-kernel weight, is presented in Table 7. The increase in the amount of shriveled grain, due to increasing head surface area colonized by S. nodorum and S. tritici, was similar to the effects observed for the individual pathogens on susceptible hosts (Eyal, 1972; Sharp, Brönnimann and McNeal, 1972). The lack of effect of foot rot on seed quality was not surprising since it does not reside, as do the Septoria spp., in the tissues primarily responsible for producing the photosynthate that is translocated to the grain (Wardlaw, 1968). P. herpotrichoides has been observed to reduce mean-seed weight when lodging occurs (Scott and Hollins, 1974), but no lodging occurred in this study.

The three-dimensional graph of the variable total grain weight (Figure 5) shows the significant culm by head infection interaction (Table 6). Foot rot at the slight or moderate levels did not affect total yield significantly. At those levels of foot rot, each increasing level of Septoria spp. head infection produced significant reductions in total yield. Foot rot caused a significant yield reduction only when Septoria spp. head infections were slight and foot rot was severe. Any effect due to severe foot rot at the higher levels of Septoria spp. head infections was masked by the two-way reduction

of total yield (quantity x quality) caused by Septoria spp. Similarly, the effect due to increasing levels of Septoria spp. head infections among the tillers with severe foot rot was not as pronounced as at the lower foot rot levels.

The three-dimensional graph of the mean number of kernels per head (Figure 6) shows the effect of a very strong interaction term (Table 6). Severe infections by either P. herpotrichoides or Septoria spp. reduced kernel number per head significantly when the other pathogen was at the slight or moderate level. The foot rot by Septoria spp. infection combination of severe x severe was no worse in its effect than the moderate x moderate or severe x moderate infection combination. This could be interpreted as a lower limit of reduction, or could have been due to a poor estimate of the effect. The severe x severe infection combination had the lowest number of observations in the data matrix (Table 5). There was also a great deal of variation so that a small sample size would not estimate the mean effect for that combination as well as the larger samples did for the other combinations. "White heads", a common symptom of severe foot rot, are spikes in which all the florets have aborted. Some of the tillers severely infected by P. herpotrichoides in this study had no grain. This white head condition is the absolute lower limit of yield. The sample size problem for the severe x severe infection combination therefore appears to be the reason for the lack of response.

The proportion of variation that was not explained by the two disease factors and their interaction (error sums of squares/total sums of squares) for the variables, grain weight and number of kernels,

was 0.70 and 0.81, respectively. Most of this variation was due to the range in head sizes that can be found within a cultivar (Engledow and Wadham, 1923; Fraser and Dougherty, 1978; Sims and Aitken, 1979). The coefficient of determination (R^2) values for head size and grain weight was 0.43, and for head size and number of kernels was 0.74.

Ideally, head size could be used as a concomitant variable. Variance due to head size would thus be removed from the error term (in an analysis of variance), allowing a better estimate of the effect of the pathogen (Neter and Wasserman, 1974). A concomitant variable, though, must be independent of the other factors being tested. The correlations for Septoria spp. and foot rot scores with head size were -0.08 and -0.34, respectively. These correlations by themselves support the independence requirement of a concomitant variable, but there is indirect evidence in the literature that implicates foot rot as a factor affecting head size. Sims and Aitken (1979) have shown that within a cultivar, the main shoots are taller, and their heads larger than lateral shoots, thus producing more and heavier weight grain than from laterals. The length of the ear and the height of the stem are affected similarly by many environmental factors (Wardlaw, 1975). Dickens (1964) and Bruehl et al. (1968) have shown that one of the effects of foot rot is general growth debilitation, reflected by reduced shoot lengths. The variation in head size, although poorly correlated to foot rot severity in this data set, may not be entirely independent of the disease.

Foot Rot Yield Loss Threshold, Model

Yield per unit area is a function of the number of fertile tillers per unit area, the number of seed set per head and the quality of the grain (weight per kernel). Any factors that affect any of these three main components directly or indirectly will affect yield. P. herpotrichoides has been implicated as a factor in all three components under certain conditions. Greatest yield losses occur when the pathogen infects host tissue early, and when conditions are optimal for maximum lesion development, thereby killing some tillers early in the season. Foot rot will also, under these conditions, reduce the number of seeds set and will cause lodging which affects grainfill, greatly reducing seed quality. This scenario rarely occurs all in one season. It is thus important to know the minimum yield losses that can be expected for particular levels of infection, and the lowest proportion of infected tillers that will cause significant yield losses.

The conditions, under which the single-tiller study was conducted, were ideal for determining the yield loss threshold. The plants were sown late and inoculated late, limiting infection somewhat. There was also little lodging and abundant moisture at the grainfill period. The main effect on yield therefore was through the reduction in the number of kernels as shown in the previous section. The major element missing that is necessary for determining the yield loss threshold was discrete replicated groups of tillers with a range of infection severity. The initial estimates of a yield-loss relationship and a yield-loss

threshold could be achieved through the montecarlo simulation of replicated groups of disease severity.

The mean number of kernels per head for tillers that had severe foot rot, but little or no Septoria spp., was 31.28. Tillers that had little or no visible foot rot or Septoria spp. head infections had a mean of 52.77 kernels per head. The samples that produced those means were approximately normally distributed and had standard deviations of 16.72 and 16.92, respectively. Observations were generated that were normally distributed about those means and had the above standard deviations, using the montecarlo subsystem of the SIPS statistical package (Rowe and Brenne, 1981). The generated treatments were analyzed to determine the relative threshold for yield loss. The proportion of tillers that must have severe foot rot before significant yield loss occurs was between 10 and 20 percent (Table 8).

A yield-loss equation was developed from these generated data by first converting the yield component to a percentage, based on the mean value for no effect on the number of kernels per head in the original data. Combinations of infected and uninfected tillers were then used as the data in the regression. The resulting relationship had an R^2 value of 0.93 and was of the form:

$$YL = -1.96 + 0.44 SF$$

where YL was the percentage yield loss, and SF was the percentage of infected tillers with severe foot rot. Some of the data points used to develop this regression had negative yield losses when none of the tillers had severe foot rot. These negative values are to be expected

because the zero yield loss was defined by a mean value. If the highest value of number of kernels per head was used to define the zero yield loss level, then the equation would predict that no disease would cause a significant amount of loss most of the time.

Single Tiller-Plot Scale Comparisons

The per unit area or plot-scale data are summarized in Table 9. The two different inoculum levels resulted from the plot design. The uninoculated plots were adjacent to inoculated plots, and since the effective dispersal range for P. herpotrichoides is 1 m (Rowe and Powelson, 1973), the center rows had less incidence and therefore fewer tillers with severe lesions.

The plot-scale data were analyzed as a 2 x 2 factorial in which each factor, inoculum and fungicide applied, had two levels. There were no significant differences between the 1000-kernel weights, indicating a lack of differential effect of foot rot or Septoria spp. on the treatment combinations. This corresponds to the single-tiller results. It was also expected because the harvesting procedure generally loses the poor-quality, light seed, and the treatments are not known to produce significant effects on severity of Septoria spp. infections (Jones and Jenkins, 1978; Cook, 1980; Jones, Dolezal and Collins, 1980; Sciumbato and Edwards, 1980). The effect of head infections was reflected in the overall depressed yields attained. In a parallel disease progress experiment in eastern Oregon, yields from plots that were not infected by Septoria spp. averaged 5000 kg/ha (unpublished).

The main effects, foot rot inoculum and fungicide level, were significant with respect to the percentage of tillers with severe foot rot. The interaction between the two factors was not significant, therefore more inoculum produced more disease, and use of the fungicide reduced disease regardless of the inoculum level (Table 9). Total yield, however, was affected only by the application of the fungicide. The increase in yield occurred regardless of the inoculum level. There was apparently not enough of a difference between disease levels at the low and high inoculum dosages to cause a significant difference in yield (Table 9).

The plot-scale data (Table 9) showed that a mean disease-severity difference of 13.9 percent (individually 10.9 and 16.9 percent for the high minus low inoculum levels) did not produce a significant yield loss. This corresponds to the yield-loss threshold obtained by the montecarlo technique, and also supports the contention that the only yield factor being affected by foot rot under these conditions was the number of kernels per head.

The yield-loss equation and its associated variance components were used to get a prediction interval (Neter and Wasserman, 1974) for yield losses on the plot scale. The actual yield losses, calculated as a percentage of the yield attained in the low inoculum-fungicide sprayed plots, were within the prediction intervals (Table 10). Assuming that no infection would yield 3 to 5 percent higher (Scott and Hollins, 1978) than the highest yield in Table 6 and use that as the base level for calculating yield loss, then the montecarlo yield-loss model underestimates the yield loss at the 30 percent severe foot rot level. Fehrmann, Reinecke and Weihofen (1978) have

shown that MBC-producing fungicides like benomyl can give up to a 10 percent yield increase even in the absence of P. herpotrichoides. Since the yield-loss calculation of Scott and Hollins was based on yields in fungicide-treated plots, the former method of calculating yield loss appears to be more realistic.

The single-tiller assay has helped to determine several points of importance with respect to the implementation of realistic disease-management schemes. The yield-loss threshold, 10 to 20 percent severely infected tillers, is a target for a P. herpotrichoides disease-management program. Benefit of preventing disease development below the threshold level would not be measurable in terms of yield increases. P. herpotrichoides, even at levels that do not induce lodging and with concurrent Septoria spp. infections, needs to be considered in a management program for the damage that it can produce. The montecarlo technique can be used to relate the more detailed examination of pathogen effects on yield components to data collected on a larger scale. It should only be used as a first approximation of a comprehensive yield-loss relationship. The yield-loss relationship developed in this way provides a frame of reference for disease-severity forecasts by providing an estimate of the minimum losses that could be expected.

Table 4. Culm and head infection scores used to rate Pseudocercospora herpotrichoides and Septoria spp. infections, respectively.

Score	Infection Description		Consolidated Score
	Culm Necrosis	Head Discoloration	
0	none	none	slight
1	0-25% culm diameter	10%	slight
2	25-50% culm diameter	35%	moderate
3	50-75% culm diameter	65%	moderate
4	75-100% culm diameter	90%	severe
5	100% and collapsed	100%	severe

Table 5. Number of observations per infection combination by Pseudocercospora herpotrichoides and Septoria spp.

Septoria Head Infections	<u>P. herpotrichoides</u> Infections			Total
	Slight	Moderate	Severe	
slight	26	36	39	101
moderate	37	56	43	136
severe	12	21	9	42
Total	75	113	91	279

Table 6. Probability of significant effects of Septoria spp. head and Pseudocercospora herpotrichoides culm infections on yield components.

Factor	Yield Component Per Head		
	Grain Weight	Number of Kernels	Mean Kernel Weight
Footrot	.9842 ^a	.9887	.3426
Septoria	.9999	.9997	.9999
Footrot x Septoria	.9774	.9944	.8773

^aThe probability level must be greater than .95 to be significant.

Table 7. Effect of Septoria spp. head infections and Pseudocercospora herpotrichoides culm infections (foot rot) on mean kernel weight per head.

Septoria Score	Foot Rot Score		
	Slight ^a	Moderate	Severe
slight	0.047 x	0.041 x	0.044 x
moderate	0.028 y	0.032 y	0.029 y
severe	0.019 y	0.020 z	0.017 y

^aAll weights in grams. Means within a column not followed by the same letter are significantly different ($P < 0.05$) by the Bonferroni multiple comparisons procedure.

Table 8. Detection limit of the effect of severe foot rot, Pseudocercospora herpotrichoides, on the yield component mean number of kernels per head.

Percent Severely Infected Tillers	Mean Number of Kernels Per Head ^x
0	53.9 a
10	51.6 ab
20	49.3 b
50	41.1 c
80	35.7 d
90	32.8 d

^xAll means montecarlo generated. Means not followed by the same letter are significantly different at $P \leq 0.05$ by the Duncan's multiple range test. S.E.M. = 1.05 (df = 24).

Table 9. Effect of inoculum level and fungicide (benomyl) dose on plot-scale foot rot disease severity and yield.

Inoculum Level	Factors Fungicide (kg/ha)	Tillers With Severe Foot Rot (%) ^x	Total (kg/ha)	Yield 1000 kernel weight (g)
low	none	54	3076	40.38
low	.56	19	4164	44.27
high	none	71	3023	43.53
high	.56	30	3383	43.42

^xAll means based on ten replications.

Table 10. Predicted yield-loss intervals and actual yield losses due to Pseudocercospora herpotrichoides foot rot.

Percent Severe Foot Rot	Predicted Yield Loss Interval (%) ^x	Actual Yield Loss (%) ^y
19	-2.4 mean loss 15.3	0
30	2.5 mean loss 20.1	18.7
54	13.1 mean loss 30.7	26.1
71	20.6 mean loss 38.3	27.4

^xProbability of 0.95 that prediction interval contains the mean.

^yYield loss relative to 19 percent severe foot rot level.

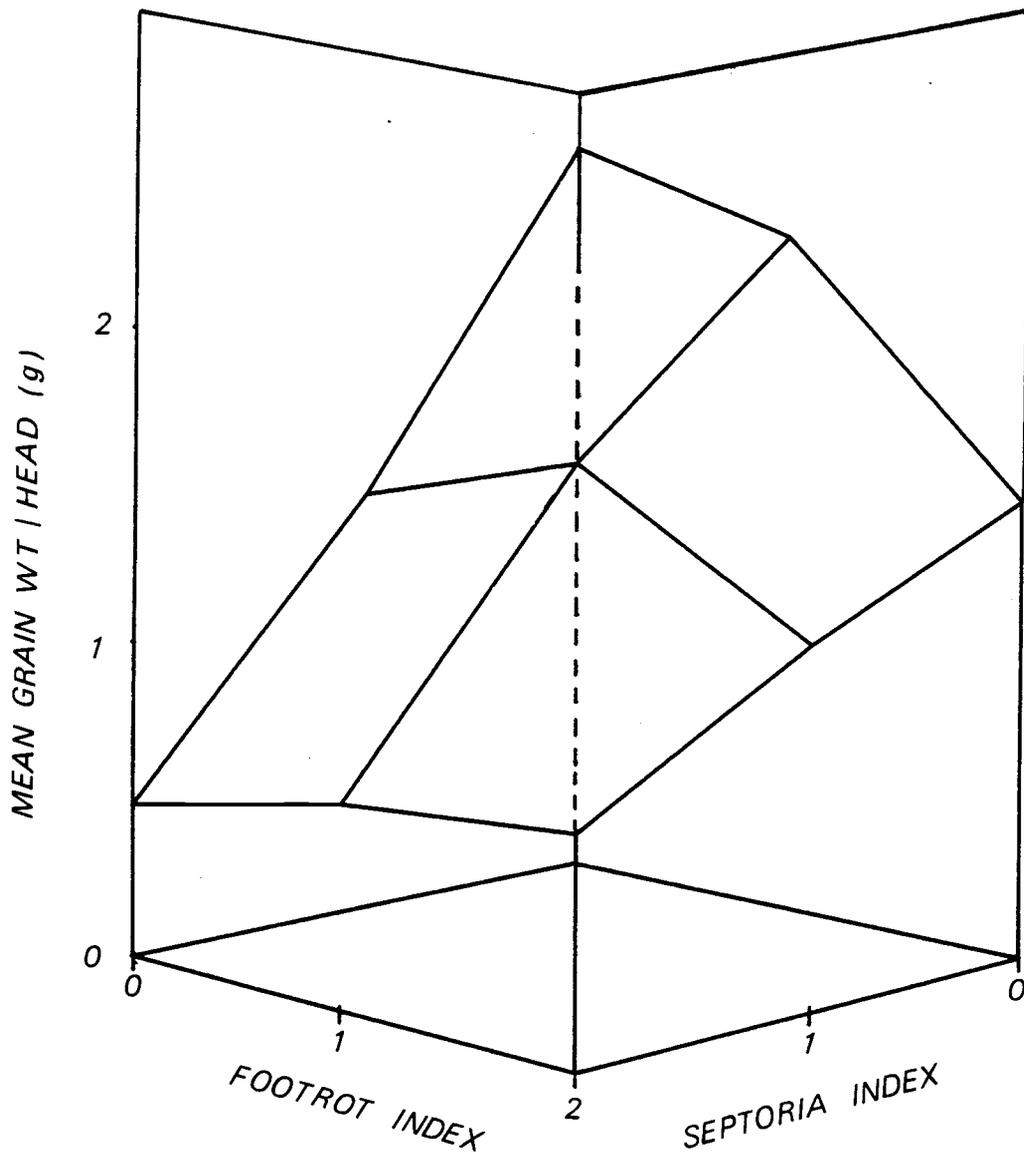


Figure 5. Total yield per head response surface. Total yield as affected by infection combinations of P. herpotrichoides foot rot and Septoria spp. head infections from 0, little or no infection, to 2, severe infection.

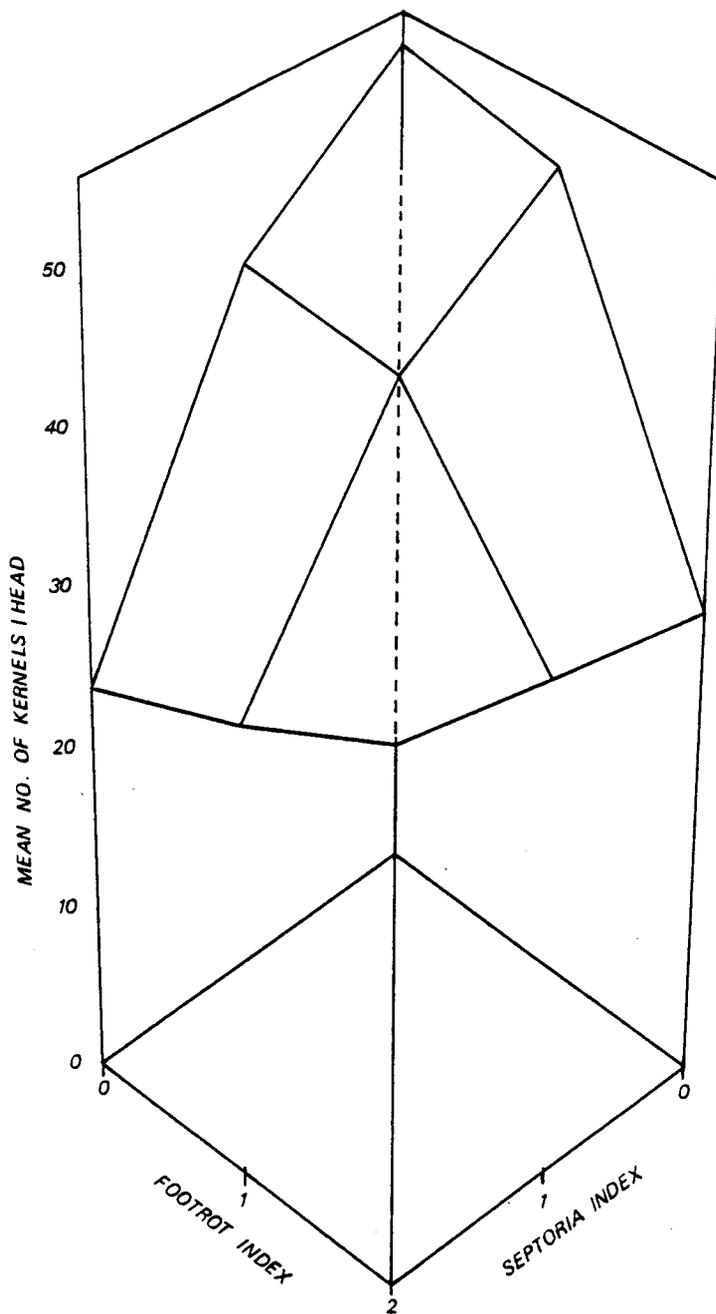


Figure 6. Quantitative yield component, number of kernels per head, response surface depicting affect of infection combinations of P. herpotrichoides foot rot and Septoria spp. head infections over the range of 0, little or no infection, to 2, severe infection.

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APPENDICES

APPENDIX 1

PSEUDOCAST DATA SHEETS
BACKGROUND

date: _____

Site: _____ ID # _____

Grower: _____ Phone _____

Cultivar: _____

Seeding date (week): _____ Seeding depth: _____

Seeding rate: _____

Herbicides: _____

Fertilizers: _____

"Normal" Yield: _____

Soil type: _____ pH _____

Site elevation: _____

Slope & Aspect: _____

Crop History: _____

Crop	Foot Rot		Other
	Presence	Losses	
_____	_____	_____	_____

last year _____

2 yrs ago _____

3 yrs ago _____

4 yrs ago _____

Surface (Sub-) Debris: _____ % Possible Inoc. Source: _____

GS (NOV 15): _____

Cultivation: _____

Date of spray application: _____

GS at spray application: _____

Weather during application: _____

Weather after application: _____

Application method: _____

Amount of product: _____

Amount of water: _____

Row spacing: _____ Tillers/foot of row: _____

Notes:

APPENDIX 2

METEOROLOGICAL DATA

The meteorological data used in the forecasting study (Chapter 3) minimum and maximum daily temperatures and daily precipitation, were obtained from the closest meteorological stations to each site. The following 13 figures are graphs of the meteorological data by meteorological station. The station code descriptions are below:

<u>Station Code</u>	<u>Description</u>
7980 STA 1	Dallas, Polk County, 1979-80
7980 STA 2	McMinnville, Yamhill County, 1979-80
7980 STA 3	Silverton, Marion County, 1979-80
7980 STA 4	Dufur, Wasco County, 1979-80
7980 STA 5	Milton-Freewater, Umatilla County, 1979-80
7980 STA 6	Pendleton Airport, Umatilla County, 1979-80
7980 STA 7	Pendleton, Br. Exp. Sta., Umatilla County, 1979-80
8081 STA 1	Corvallis, Benton County, 1980-81
8081 STA 2	Pendleton, Br. Exp. Sta., Umatilla County, 1980-81
8081 STA 3	Pendleton Airport, Umatilla County, 1980-81
8081 STA 4	Pilot Rock, Umatilla County, 1980-81
8081 STA 5	North Willamette Exp. Sta., Clackamas County, 1980-81
8081 STA 6	McMinnville, Yamhill County, 1980-81

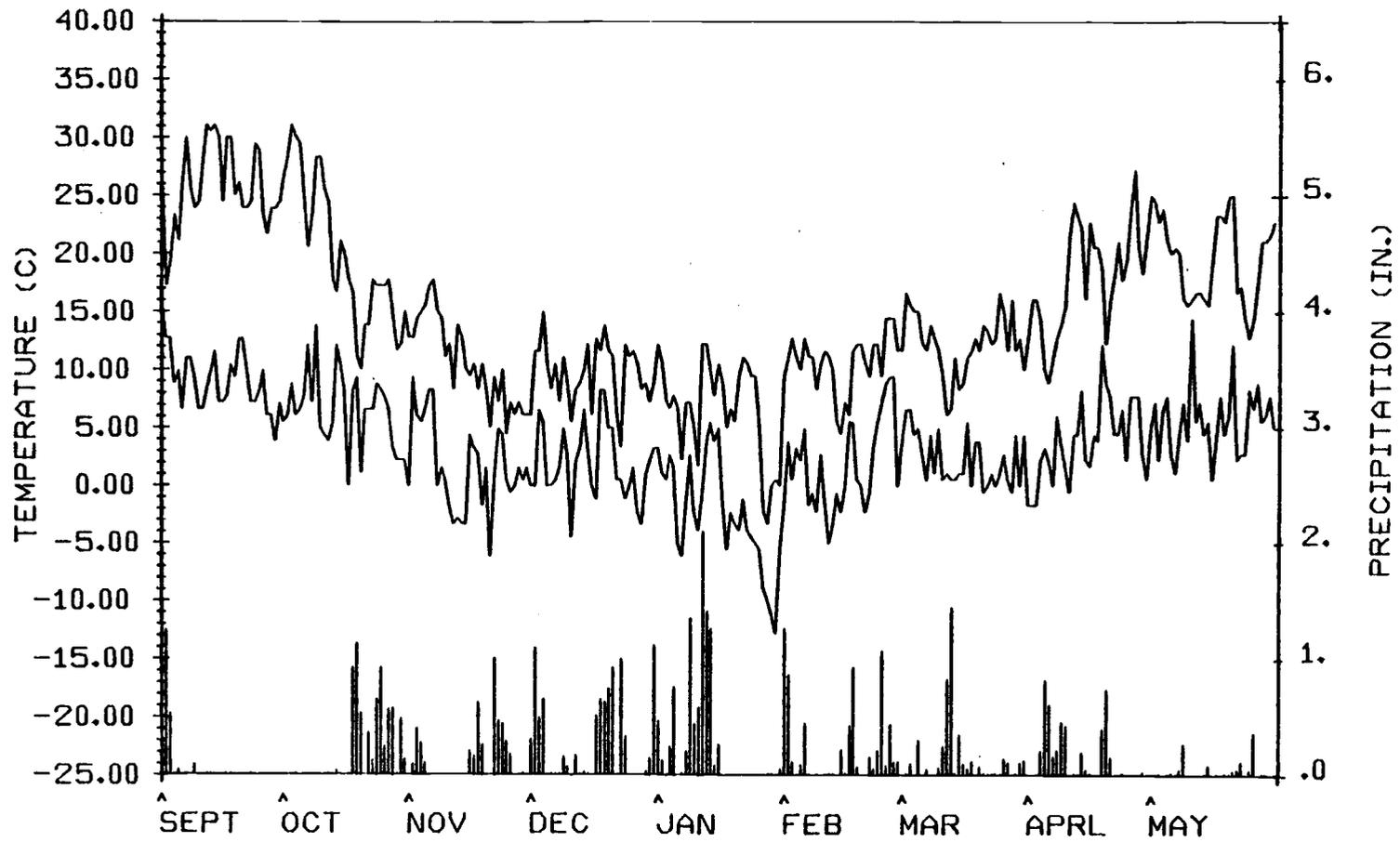


FIGURE 7. Meteorological data, Station 1, Dallas, 1979-80.

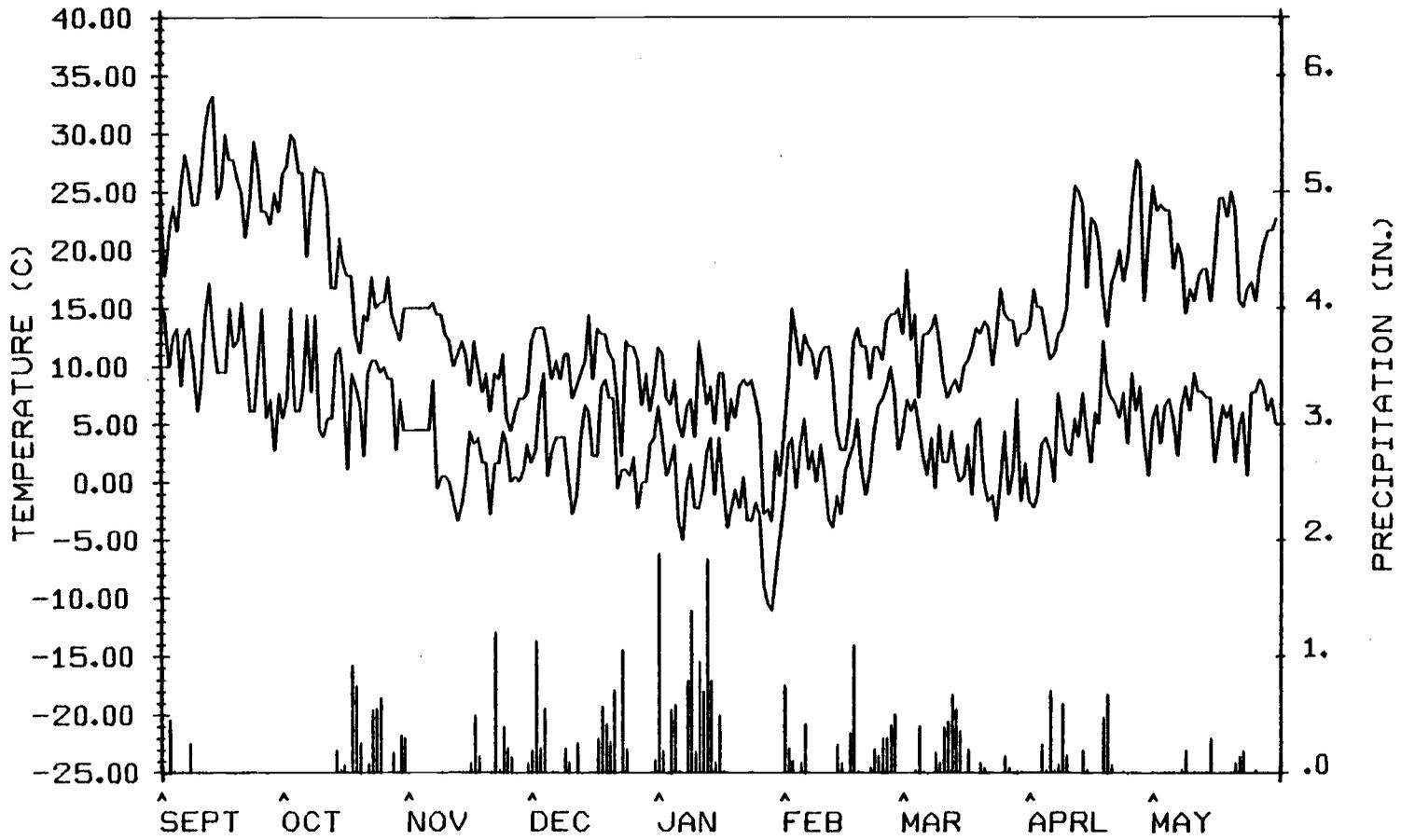


FIGURE B. Meteorological data, Station 2, McMinnville, 1979-80.

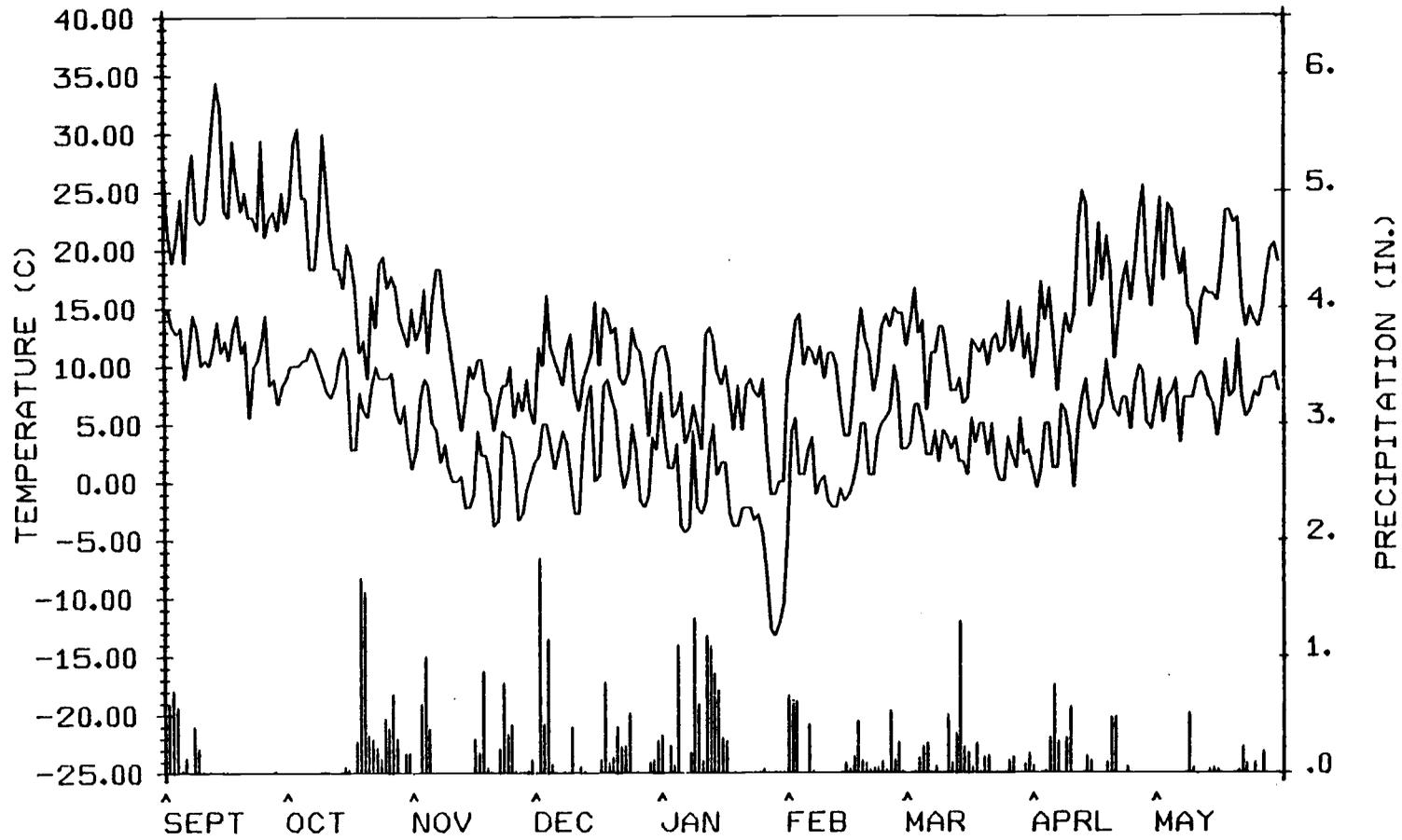


FIGURE 9. Meteorological data, Station 3, Silverton, 1979-80.

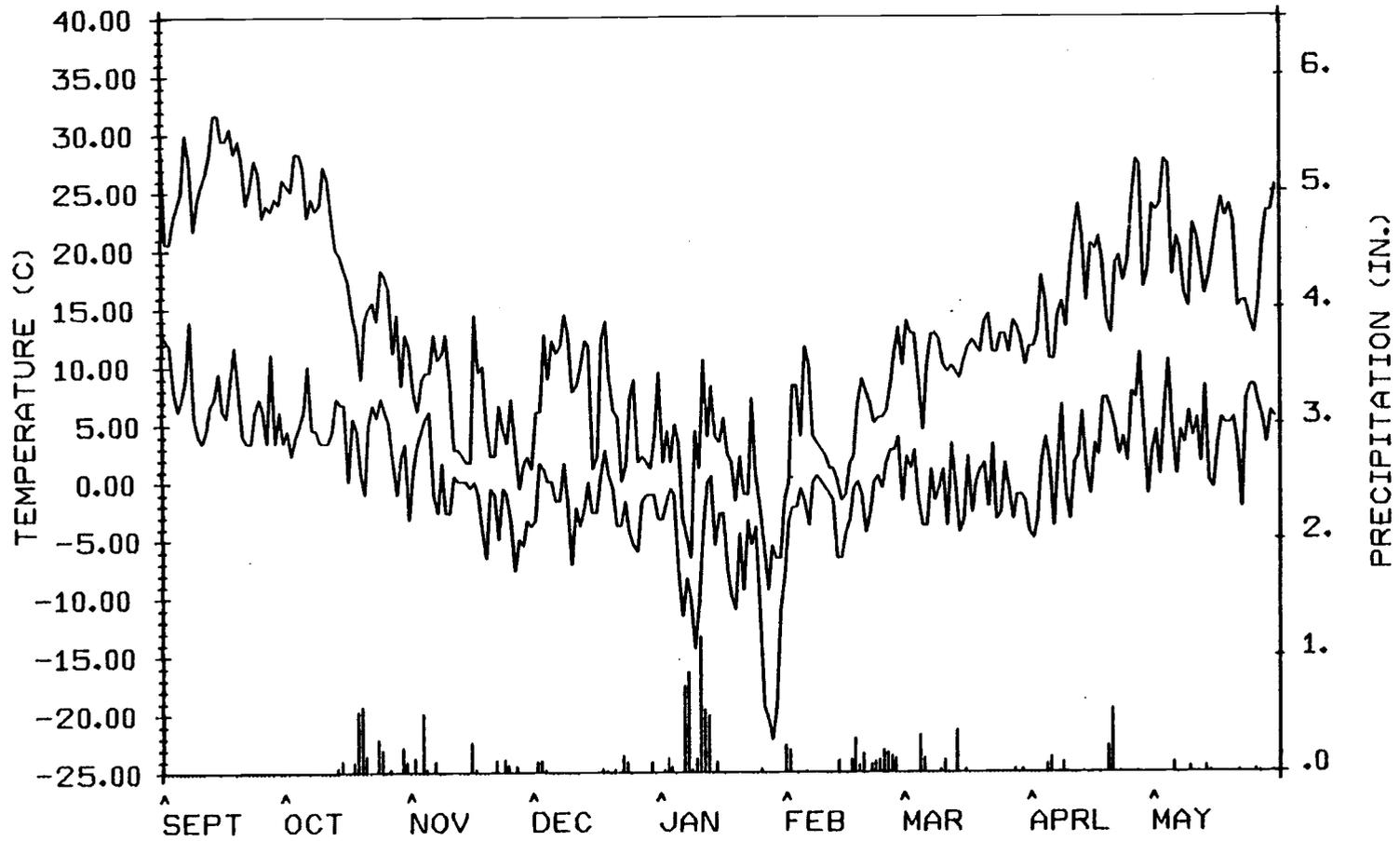


FIGURE 10. Meteorological data, Station 4, Dufur, 1979-80.

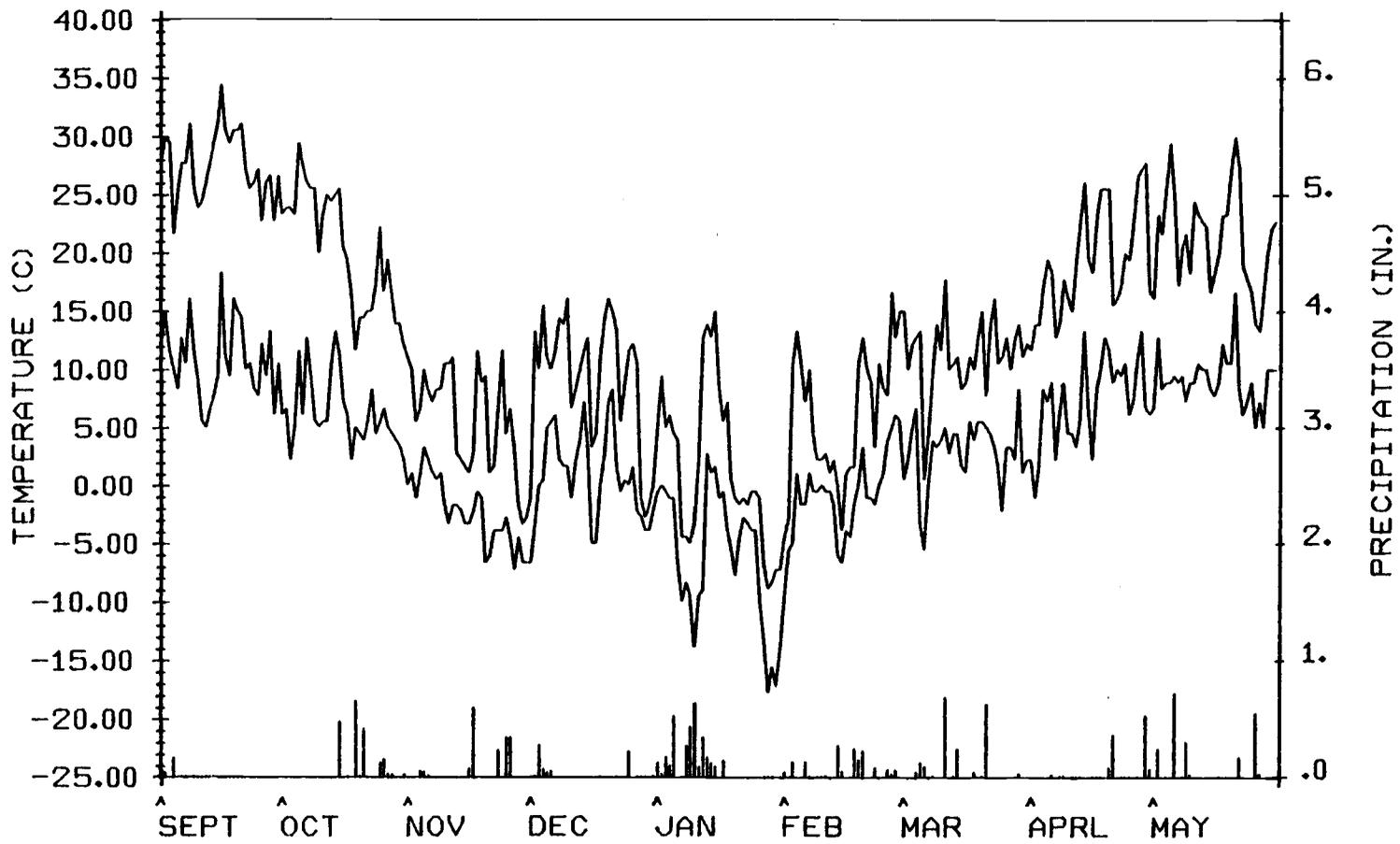


FIGURE 11. Meteorological data, Station 5, Milton-Freewater, 1979-80.

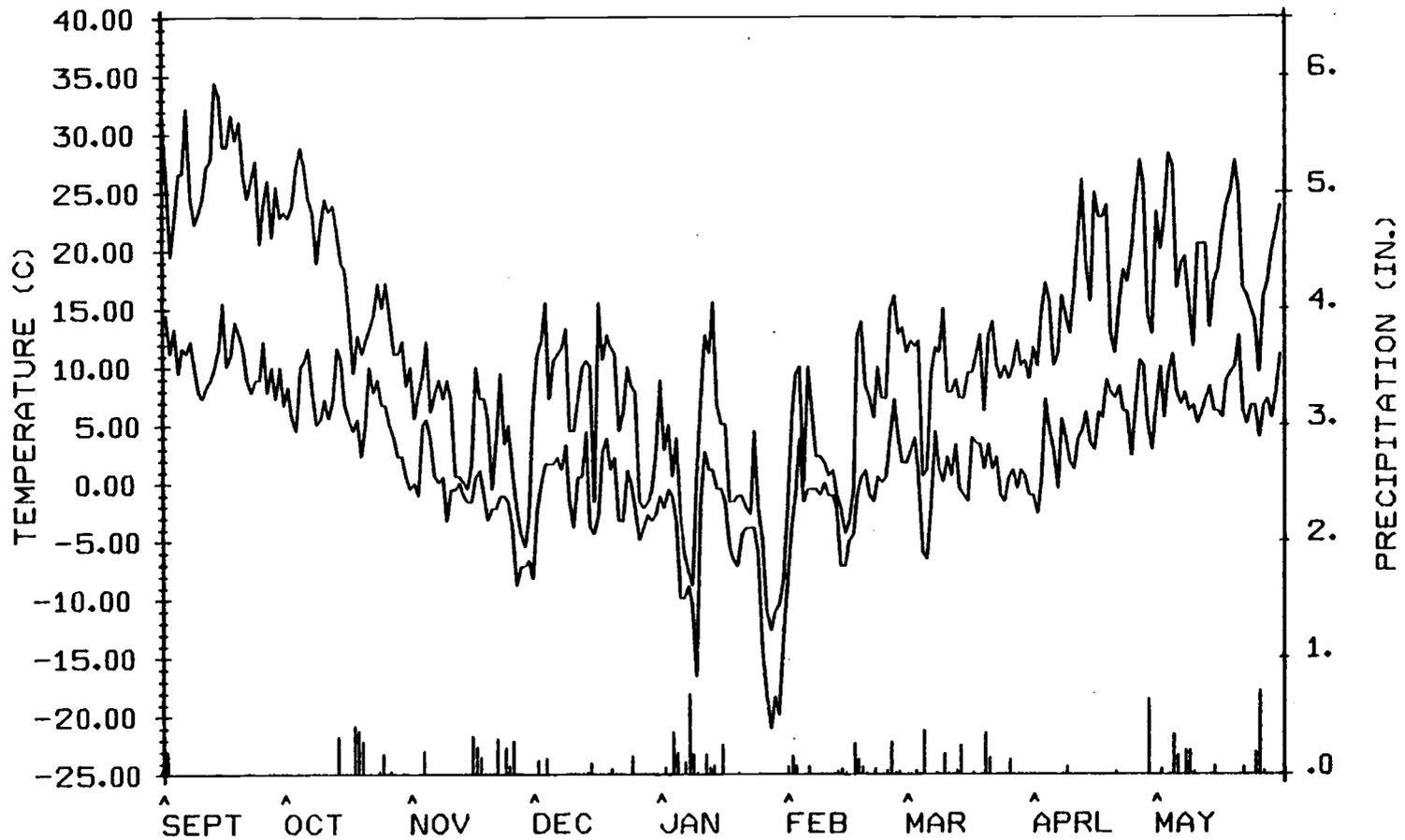


FIGURE 12. Meteorological data, Station 6, Pendleton Airport, 1979-80.

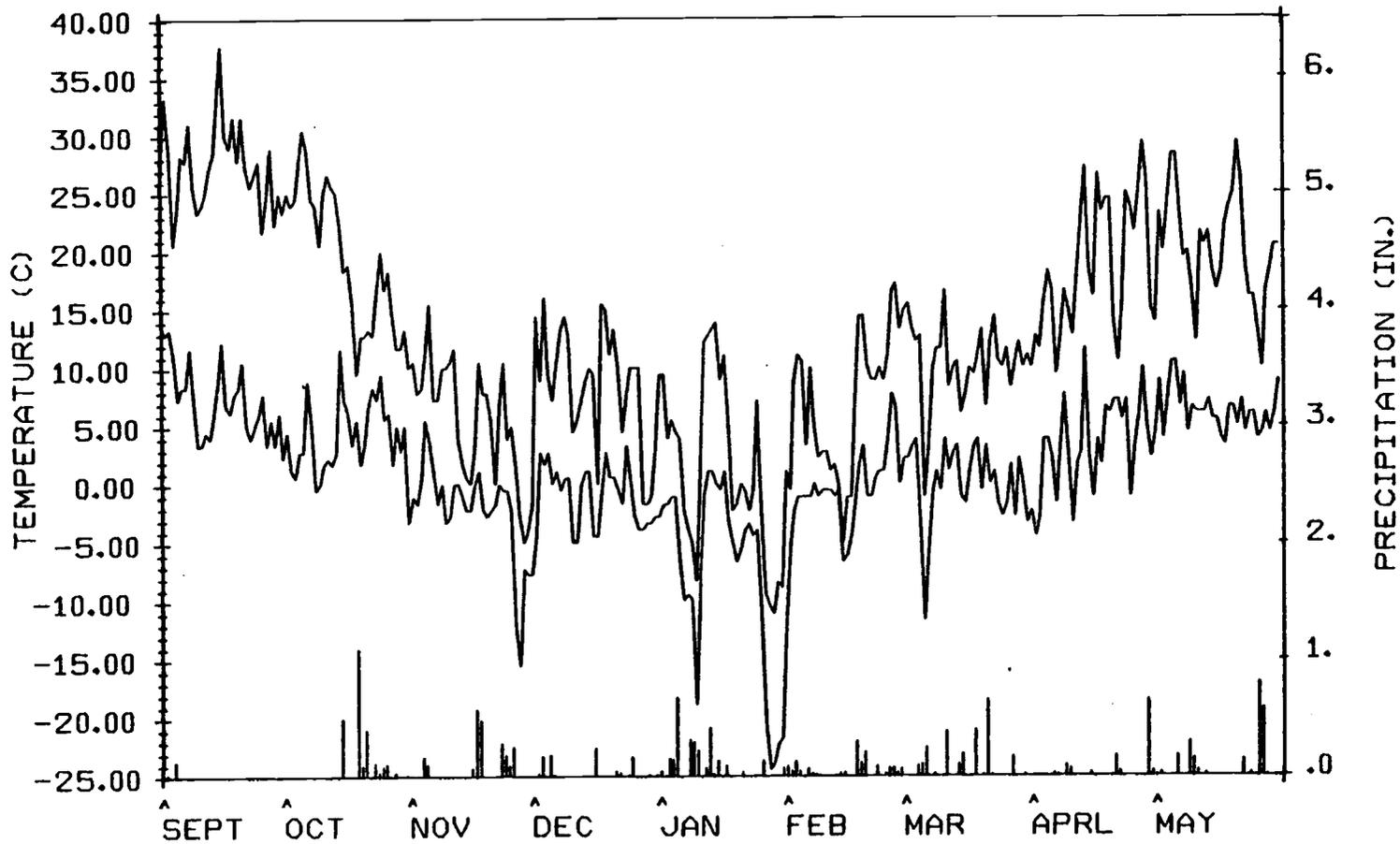


FIGURE 13. Meteorological data, Station 7, Pendleton Br. Exp. Sta., 1979-80.

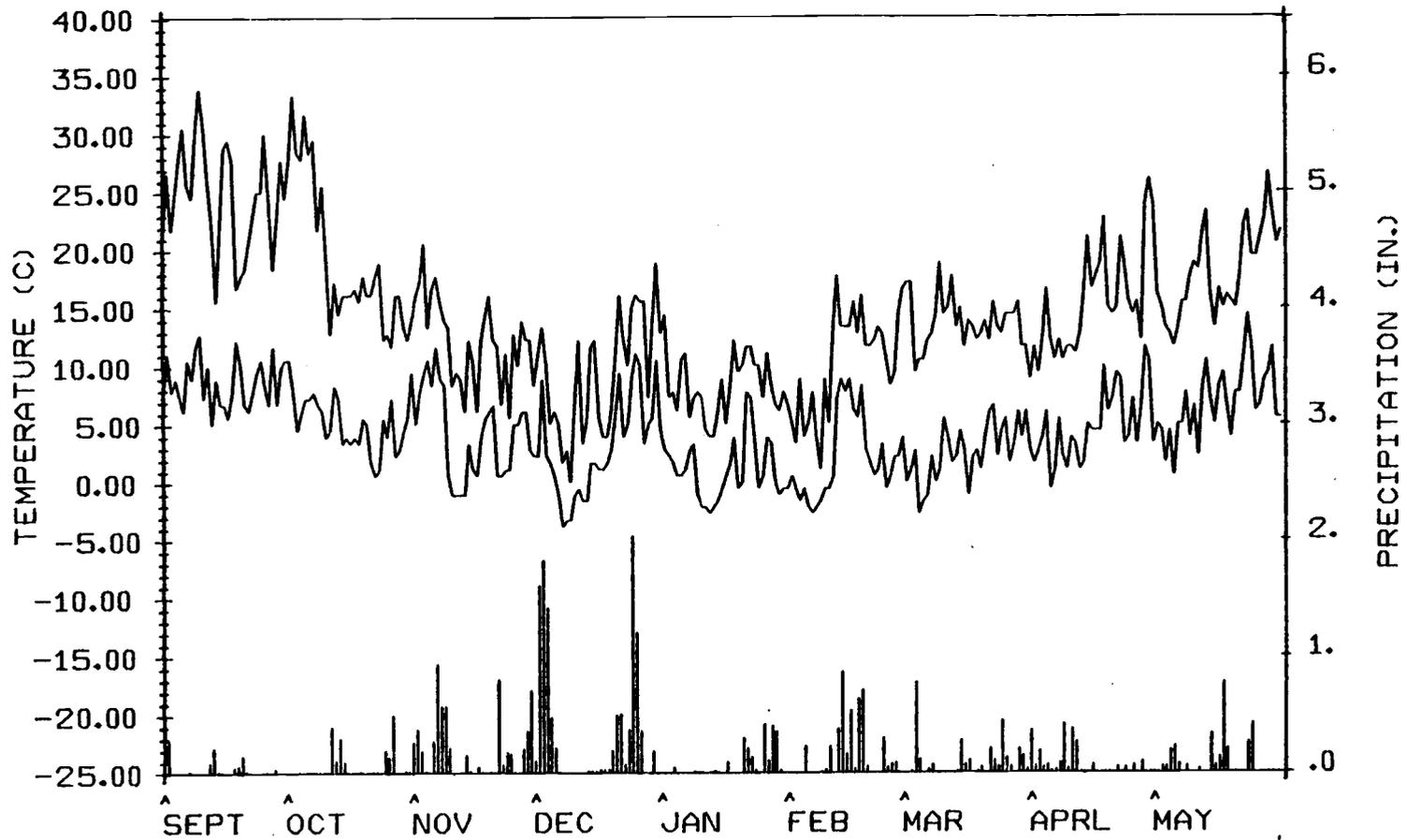


FIGURE 14. Meteorological data, Station 1, Corvallis, 1980-81.

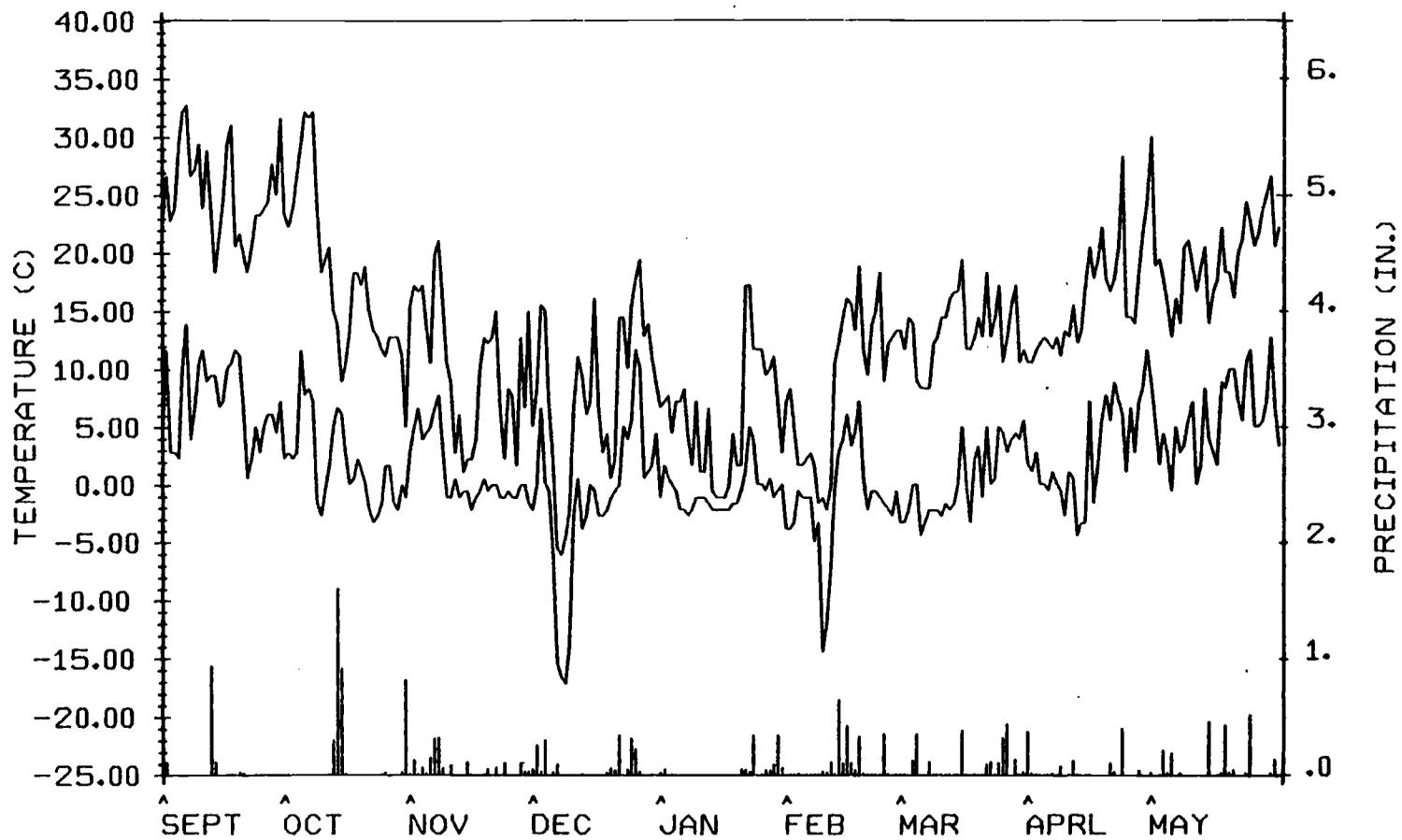


FIGURE 15. Meteorological data, Station 2, Pendleton Br. Exp. Sta., 1980-81.

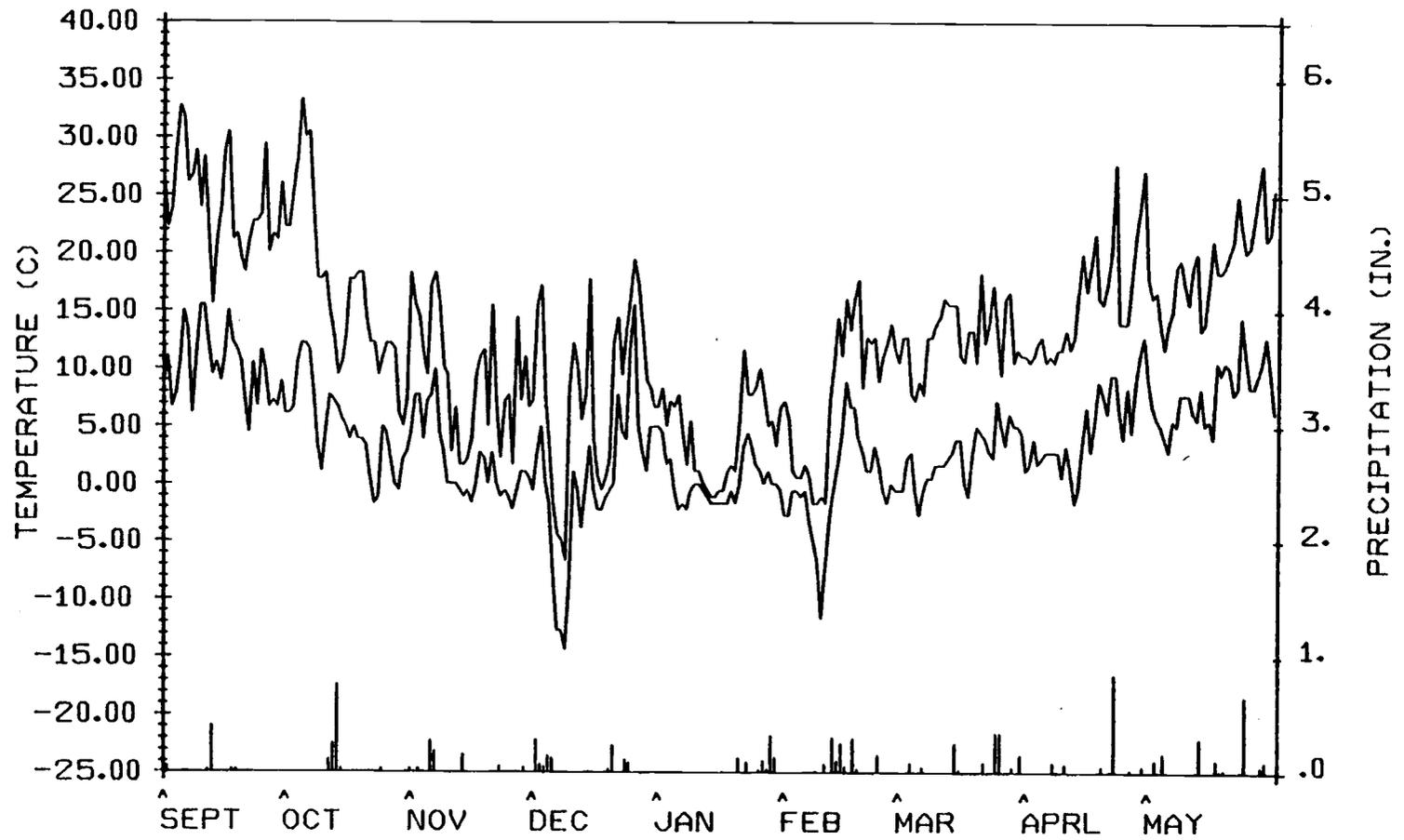


FIGURE 16. Meteorological data, Station 3, Pendleton Airport, 1980-81.

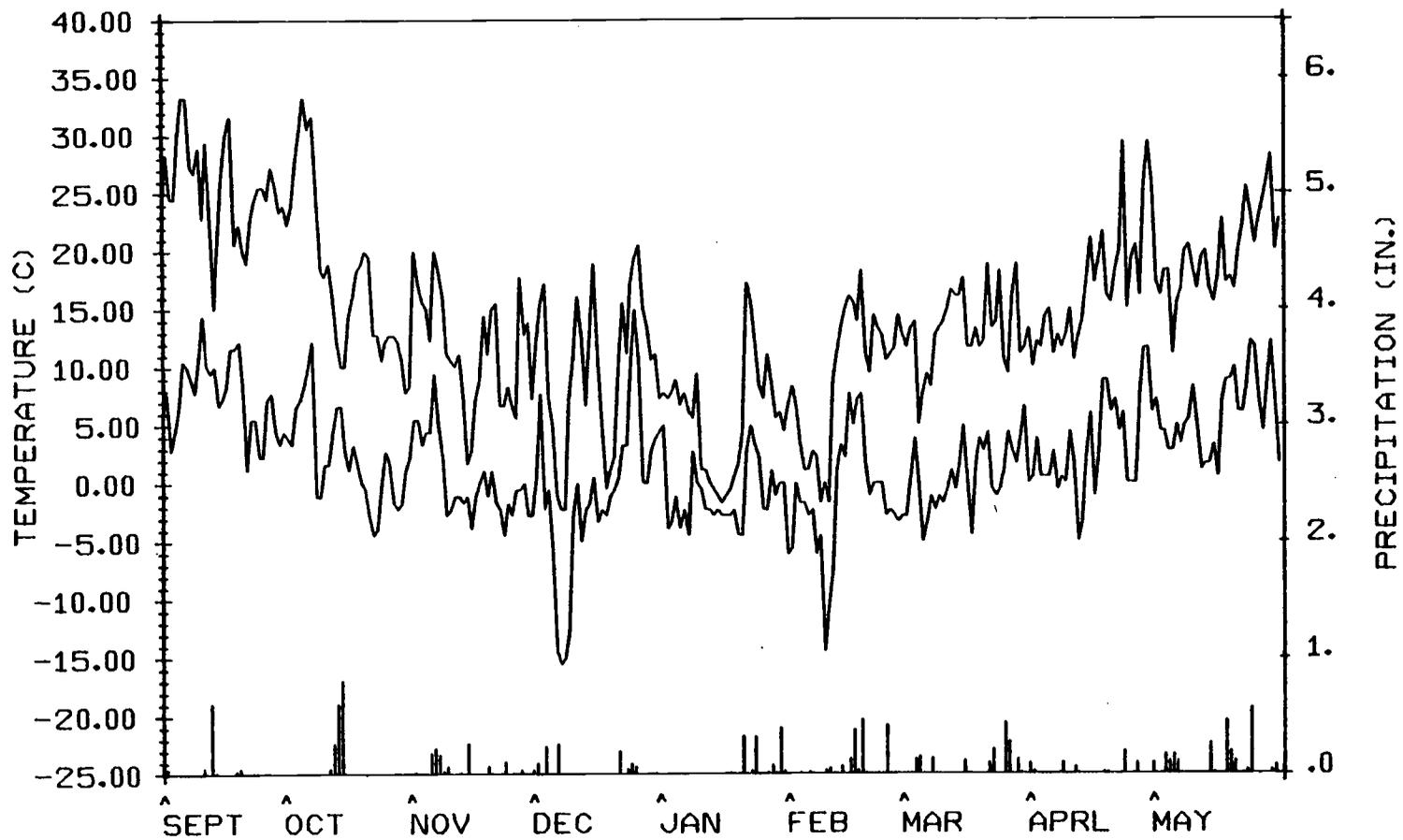


FIGURE 17. Meteorological data, Station 4, Pilot Rock, 1980-81.

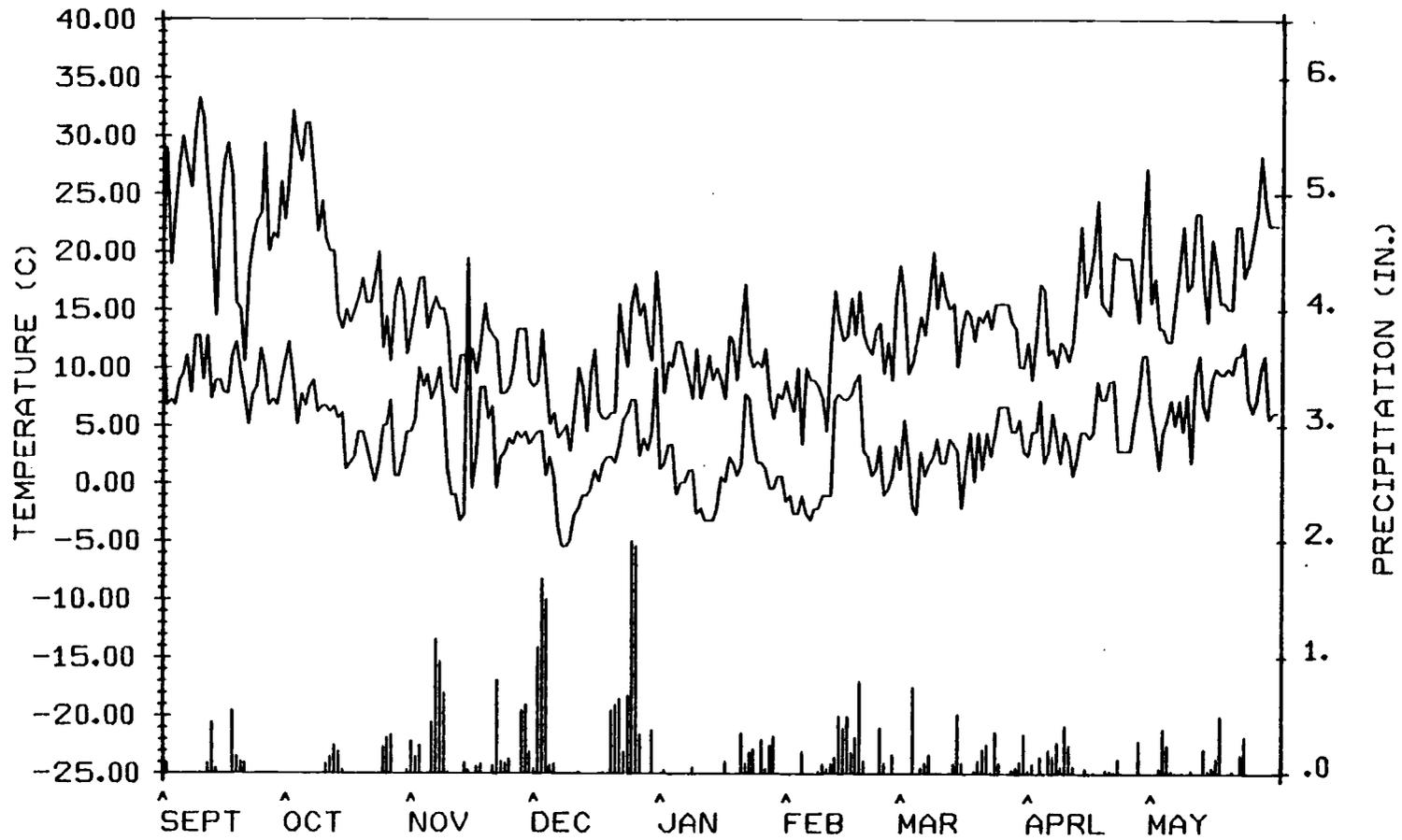


FIGURE 1B. Meteorological data, Station 5, North Willamette Exp. Sta., 1980-81.

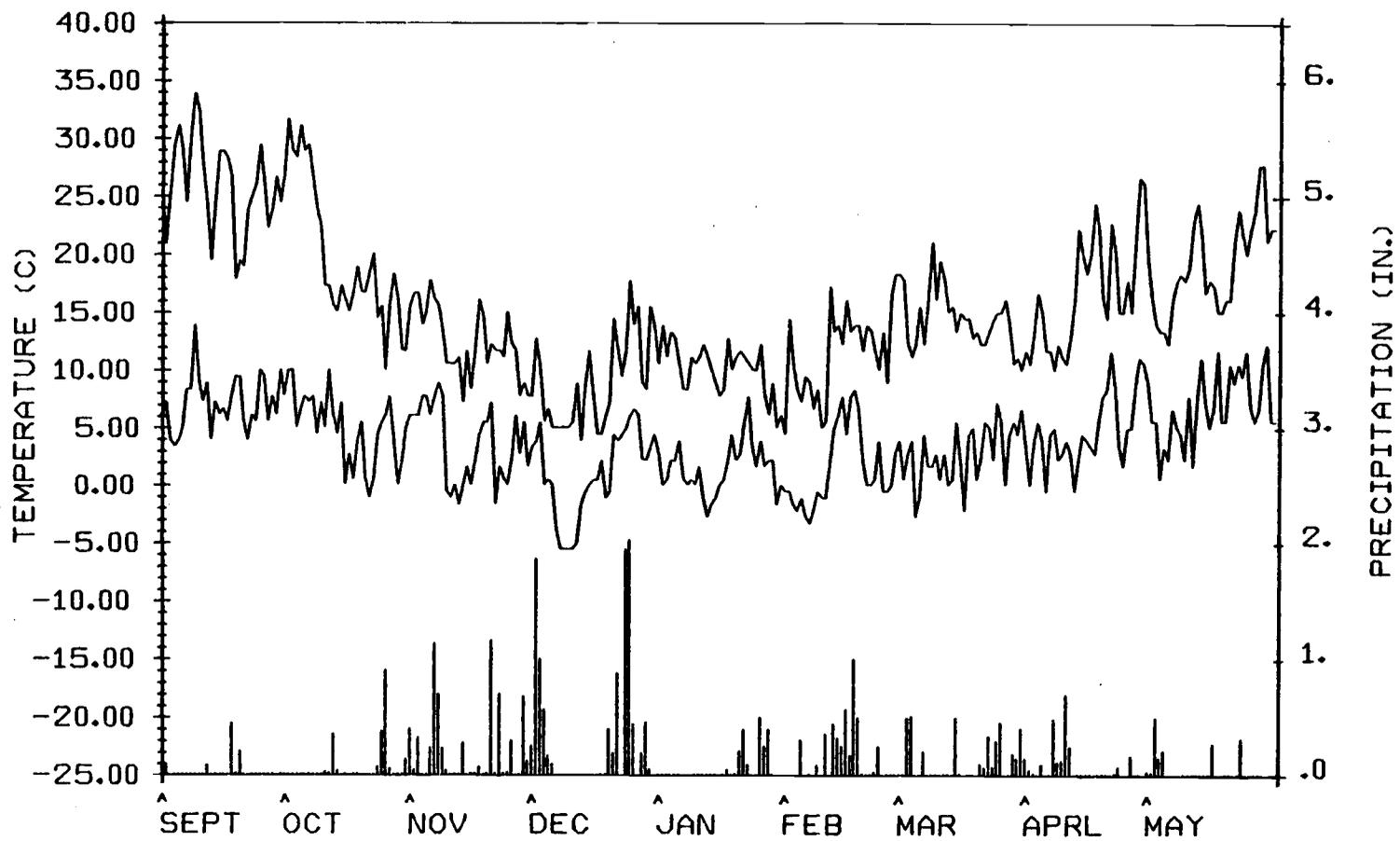


FIGURE 19. Meteorological data, Station 6, McMinnville, 1980-81.

APPENDIX 3

Functions or values used for environmental data reduction.

Effective Day Temperature: $T_{max} - \frac{1}{4} (T_{max} - T_{min})$

Effective Night Temperature: $T_{max} + \frac{1}{4} (T_{max} - T_{min})$

Wang Crop Rainy Day Criteria

1. Isolated Events

- a. ppt. > 0.20 in. = 1 Crop Rainy Day (Rc)
- b. 0.20 in $<$ ppt. > 0.15 in. and last Rc not more than 2 days ago = 1 Rc
- c. ppt. < 0.15 in. = 0 Rc

2. Continuous or Adjacent Events

- a. ppt. > 0.10 in. = 1 Rc
- b. 0.10 in. $<$ ppt. > 0.05 in., and total for 2 consecutive days > 0.20 in., then the two day total = 2 Rc if the greater amount of ppt. was on the 1st day; if greater amount of ppt. on 2nd day and no previous rain then total = 1 Rc
- c. ppt. < 0.05 = 0 Rc

Temperature Score (Tscore)

<u>Median Daily Temperature (c)</u>	<u>Bscore</u>
8-11	1
5-8 or 11-15	0.5
0-5 or 15-20	0.25

If $T_{max} > 20$ then $T_{score} = \frac{1}{2} B_{score}$

If $T_{min} < -5$ then $T_{score} = \frac{1}{2} B_{score}$, otherwise $T_{score} = B_{score}$

Rain Score (Rscore)

If 0.1 in. $<$ ppt. > 0.01 in., then $R_{score} = 0.07 + 7.78$ ppt.

If 1.0 in. $<$ ppt. > 0.10 in., then $R_{score} = 0.83 + 0.17$ ppt.

If ppt. > 1.0 in.