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Lack of uniformity in tiller and inflorescence development in tall fescue (Festuca arundinaceae Schreb.) leads to asynchronous seed maturation and difficulty in determining optimum harvest time. Little is known about the effects of cultivar, weather, diseases, and fungicides on seed development and maturation in cool season grasses. Several experiments were designed with the general objective of determining seed moisture content at windrowing for achieving maximum yields. Specific objectives were to: a) study daily and seasonal flowering patterns in relation to weather variables; b) determine the normal course of seed development and the effects of propiconazole fungicide (1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl-methyl]-1H-1.2.4 triazole) and stem rust (Puccinia graminis Pers. subsp. graminicola Urban) on seed maturation; and c) compare seed moisture content and growing degree days (GDD) as index of optimum harvesting. The research was conducted with 'Chesapeake', 'Bonanza', and 'Emperor', turf-type cultivars of tall fescue with differing maturity dates.

Hourly and daily flowering intensities were estimated by the amount of pollen collected by Burkard spore samplers. A distinct seasonal peak anthesis occurred only when variation in the daily maximum temperature during the flowering period was small. Calculation of mid-anthesis is a practical and less subjective alternative to visual determination of peak anthesis.

A two-year experiment showed that propiconazole has no effect on seed maturation in the absence of stem rust. Physiological maturity occurred at moisture contents of 400 to 480 g kg^{-1} in both cultivars. In another one-year experiment, there was evidence that rust can hasten seed maturation when it occurs before anthesis.

A three-year study, in which plots were machine-harvested six times at successively lower moisture contents, indicated that maximum yields were obtained by windrowing at moisture contents of 350 to 410 g kg^{-1}. The growing degree days accumulated after mid-anthesis was not a consistent harvest index.

A harvest timing index based on seed moisture content appears more reliable than one based in GDD for turf-type tall fescue. It does not depend on a phenological reference point and the dynamics of moisture change during seed maturation are minimally affected by rust or propiconazole.

FLOWERING, SEED MATURATION, AND HARVEST TIMING OF TURF-TYPE TALL FESCUE

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I would like to dedicate this thesis to my mother, Maria das Dores Pereira and to the memory of my father, Jose Americo Junior.

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CHAPTER 1

GENERAL INTRODUCTION

Tall fescue (Festuca arundinacea Schreb.) was introduced into the USA as a forage species during the late 1800's and use of this cool-season grass for turf increased rapidly during the 1970s. Tolerance to high summer temperatures, capacity for growing at low temperatures, good ground cover, and persistence under less intensive management make tall fescue a popular turf species (Murray and Powell, 1979).

Tall fescue seed production is a traditional activity in Oregon, and the area harvested for seed in 1992 was estimated at 34,116 ha. The tall fescue seed crop had a value of US $ 33 million and ranked third among the grass and legumes seed crops in Oregon (OSU Extension Service,1992). Most of the seed production technology for this species was developed during the late seventies for early-maturing forage-type cultivars (Youngberg and Wheaton, 1979). The release of new turf-type cultivars with a range of maturity dates, new diseases, new pesticides that potentially interfere with plant physiology and phenology, and a limitation on open-field burning have changed the tall fescue seed production situation and justify the reviewing of existing seed production technologies.

Harvest timing is one of the concerns of grass seed growers. It affects quality and quantity of harvested seeds and a wrong decision regarding harvest time can invalidate year-long efforts toward maximum productivity. Definition of the correct harvest timing in cool-season grasses is difficult because seed maturation is not uniform and the seed shatters when mature (Andersen and Andersen, 1980). Theoretically, the optimum harvest time occurs when the increase in seed weight from maturing seeds does not compensate for losses caused by the shattering of mature seeds. Research can address the harvest timing problem through: a) studies on flowering time as a reference point for time-related harvest indexes; b) studies of factors affecting duration of seed maturation processes; and c) development of more reliable harvest indexes.

Flowering in grasses occurs over a period of time and the day with the highest number of opened flowers, or "day of peak anthesis", is used to define the time of flowering in grasses. Day of peak anthesis, which is based on visual estimation, is used as a reference point for timing of seed maturation and for harvest. Visual estimation of peak anthesis is a subjective decision which is not always reliable. Also, day-to-day variation in flowering intensity caused by weather conditions (Jones and Newell, 1946; Emecz, 1962) imposes further restrictions on the visual determination of peak anthesis. It is necessary to improve the visual method for peak anthesis determination and/or adopt alternative and less subjective indicators of time of flowering in tall fescue seed crops.

Stem rust disease was first observed in tall fescue seed crops in 1989 (Welty, 1990) and control measures are recommended to avoid yield losses. Propiconazole, a fungicide commonly used for stem rust control, interferes with the synthesis of gibberellic acid in plants (Buchenauer, 1987) and can potentially influence the progress of seed maturation in grasses. There is evidence that rust affects the seed maturation process in wheat (McGrath and Pennypacker, 1991).

Farmers rely on harvest indexes based on seed characteristics such as color, moisture content, and degree of shattering, and on time-related indexes such as days after flowering, to make decisions on when to harvest a seed crop. The existing harvest index for tall fescue is based on seed moisture content and was developed for 'Alta', an early-maturing forage-type cultivar of tall fescue (Klein and Harmond, 1971). It is not known if this index still applies for the new turf-type cultivars, mainly the late maturing ones. Days after peak anthesis is not a reliable indicator of optimum harvest timing because of year-to-year variation in seed development. Considering that daily temperature influences seed maturation (Bean, 1971), Andersen and Andersen (1980) suggested that an alternative time-related harvest index, based on number of growing degree days accumulated after peak anthesis, would be less variable than days after anthesis. With new restrictions on open field burning, the control of volunteer plants became a more important problem. Correct harvest timing reduces seed losses and, indirectly, reduces the population of volunteer seedlings in succeding seed crops.

The general objectives of this research were to study tall fescue seed maturation and determine proper harvest timing for maximum yields in cultivars of turf-type tall fescue with a range of maturity dates. Specific objectives were:

a) to study seasonal and diurnal patterns of flowering using a mechanical spore sampler and to use this information to improve the precision of visual estimation of peak anthesis. This study is described in chapter I.

b) to study the effects of propiconazole fungicide and stem rust disease on seed maturation of tall fescue as described in chapter II.

c) to determine harvest indexes for turf-type tall fescue based on seed moisture content and to study the feasibility of a time-related harvest index based on growing degree days accumulated after peak anthesis. Chapter III covers this subject.

CHAPTER 2

LITERATURE REVIEW

Flowering Patterns in Grasses

Flowering or anthesis in grasses is associated with the swelling of the lodicule (Booth, 1964). This floral structure has the capacity to act as a pulvinus and, when the lodicule becomes turgid, the lemma is forced outward while the anthers are exposed by the rapid growth of the filaments. After anthesis, the lodicules collapse and the flower closes. Lack of uniformity in the anthesis of florets in the inflorescences and in the population of tillers makes the flowering extend for a long period (Anslow, 1962). Peak anthesis, or the day with the highest number of opened flowers, is used to indicate the timing of flowering in studies of post-anthesis events and for management purposes in cool season grasses.

Wind pollination is the type of abiotic pollination prevailing in the Poaceae. In this type of pollination chances of pollen arriving at the stigmatic surfaces are optimized by exposition of flowers above the leaf mass and by the existence of dry and warm weather conditions (Dafni, 1992). The anthers of wind pollinated species dehisce when temperature is increasing and this behavior applies to daily and seasonal temperature variations (Faegri and Pijl, 1979).

The need to increase crossing efficiency in breeding programs motivated the initial interest in the flowering patterns of grasses (Emecz, 1962; Jones and Newell, 1946; Jones and Brown, 1951). Jensen (1976), however, measured seasonal distribution of flowering with the objective of determining seasonal peak anthesis. These studies followed two approaches. Flowering pattern was measured by hourly counts of the open flowers in a plant (Emecz, 1962) or inferences about flowering pattern were based on the number of pollen grains collected on slides or glass tubes exposed in the field during the flowering period (Jones and Newell, 1946; Jones and Brown, 1951; Jensen, 1976). Although one of the cheapest methods of pollen sampling, exposing of slides can be difficult if hourly sampling is needed and results are influenced by the dynamics of pollen shed (Ogden et al., 1974).

According to the historical review presented by Jones and Newell (1946) the influence of weather variables on the flowering pattern in grasses was evident since the initial studies and daily flowering pattern was attributed to the temperature and amount of moisture in the atmosphere (Gregor; 1928) or to the level of daily radiation (Hyde and Williams, 1945).

Later studies showed, however, that temperature was the driving force controlling anthesis in grasses (Emecz, 1962). Daily flowering in grasses only occurs after plants have been exposed for a period of time to temperatures and light intensities above a threshold level. For example, a threshold temperature of 17 ^{o}C with 3600 ft.c of light during 5 h was necessary for the flowering of S170 tall fescue in England (Emecz, 1962). Jones and Newell (1946), studying daily and seasonal flowering patterns in a group of grass species in Nebraska, indicated that flowering in tall fescue (Festuca arundinacea Schreb.) occurred only when temperature was between 18.5 and 30 ^{o}C. This species exhibited a maximum flowering at approximately 26 ^{o}C and temperature had to be favorable during three to four hours in a day before blooming occurred. In this species flowering was reduced at temperature of 14.5 to 15.7 ^{o}C. These same temperatures restricted flowering of perennial ryegrass (Lolium perenne L.) in New Zealand (Hill, 1971).

The response of the cool season grasses to daily temperature and the variability of this parameter during spring made the seasonal pollination cycle of these grasses to be characterized by days with heavy flowering alternated with days with low flowering (Jones and Newell, 1946). This variability in seasonal flowering pattern was also evident for meadow fescue (Festuca pratense Huds.) and Jensen (1976) commented that in some years this variability would prevent the occurrence of a defined seasonal peak anthesis. Accordingly to Jones and Newell (1946), Kentucky bluegrass (Poa pratensis L.) was the only species able to flower in cold weather conditions with flowering increasing to a well defined seasonal peak and decreasing thereafter. Glasshouse studies also showed that higher temperatures tended to reduce the length of the flowering season in tall fescue (Bean, 1971).

Timing of daily peak anthesis is characteristic for each species. For instance, daily peak anthesis for tall fescue was observed at 1430 h in USA (Jones and Newell, 1946; Jones and Brown, 1951) and at 1508 in England. In contrast, timothy (Phleum pratense L.) had peak anthesis at 0548 while with different cultivars of perennial ryegrass peak flowering occurred from 1236 to 1520 (Emecz; 1962). These authors found that, in general, high temperature and stronger light intensities tended to advance the timing of daily anthesis within the day. Hill (1971) reported, however, that night temperatures above 10 ^{o}C caused an earlier onset and reduced duration of daily flowering in perennial ryegrass. Emecz (1962) commented that weather factors tended to alter temperature at the plant level, and suggested that temperature could be the only weather parameter considered in flowering studies in grasses.

As a general tendency, daily peak anthesis occurs in the morning hours for warm season grasses while cool season grasses have peak anthesis in the afternoon. Timothy, Kentucky bluegras, Secale cereale L., and Panicum virgatum L. were exceptions to this tendency (Jones and Newell, 1946). Timing of daily peak anthesis also depended on the intensity of pollen produced in the previous days. Normally, daily peak anthesis was delayed in days preceded by a day with heavy flowering or advanced in days following periods of little or no anthesis in Russian wildrye grass (Elymus junceus Fisch.)(Dotzenko and Stegmeier, 1959).

Response to rain was specie related and while some species, like ryegrass, immediately stopped flowering in case of rain, others, like tall fescue, were sensitive but cessation of flowering was not as immediate (Emecz, 1962). In a third group, composed of Dactylis, Phleum, and Alopecurus, flowering did not stop because of rain. An opposite response was found for wind in these groups and, while Lolium was insensitive, Phleum stopped flowering with strong winds.

Cool-season grasses were classified in two groups in relation to the flowering response to weather conditions (Emecz, 1962). Group I, called "quick staminating" is characterized by plants which need a short period of exposure to suitable conditions before anthesis occurs, but need temperature and light intensity above the threshold level for anthesis to continue. Opening of the palea is very rapid and anthesis in this group is completely dependent on the prevailing weather conditions. Lolium and Festuca belong to this group. Group II, or "slow staminating", requires a longer period with suitable conditions before anthesis occurs (8 to 10 h) but are less responsive to weather factors once daily flowering starts. This group respond to conditions existing during the previous day and species of Dactilys, Phleum and Alocoperus belong to it.

Characteristics of Seed Development

Seed Weight

The final weight per seed, a component of seed yield in grasses, is dependent on duration and rate of seed filling. Information on the responses of these parameters to environmental and management factors allows a greater understanding about the formation of the final seed yield. With grasses, which lack uniformity during the maturation process, a knowledge of factors affecting post-anthesis events provides a basis for decisions regarding harvest timing. This information might also be relevant for phenological modeling.

Inferences about the parameters of seed growth in cool season grasses were obtained mainly from graphs describing the dynamics of seed development (Grabe, 1956; Hyde et al., 1959; Hill and Watkin, 1975; Hebblethwaite and Ahmed, 1978). Those parameters can also be inferred from regression models fitting the seed growth data as commonly used for small grains (Sofield et al. 1977a; Gebeyehou et al. 1982; Hanft and Wych, 1982; Darroch and Baker, 1990) or as used by Bean (1971) in glasshouse studies of tall fescue seed development.

Seed development occurs in 3 phases. After pollination, there is a "lag phase" in which cell division occurs and increase in seed dry weight is slow. The second phase or the "linear phase" of growth, ends at the achievement of maximum seed dry weight or physiological seed maturity (Shaw and Loomis, 1950). After physiological maturity, during the third or "ripening" phase, there is no further increase in seed dry weight (Grabe, 1956; Hyde et al., 1959). The weight of the husks surrounding the caryopses does not change during the seed growth (Andersen and Andersen, 1980; Scott et al., 1983).

In perennial ryegrass the first phase of seed growth was 10 d long while the linear growth phase lasted for 10 to 14 d. The third phase was the shortest with 3 to 7 d (Hyde et al., 1959).

Scott et al. (1983), in a detailed study of seed development in barley (Hordeum vulgare L.), reported that the first exponential phase of growth lasted for 10 d although it was difficult to differentiate the end of this phase from the beginning of the following linear phase. Approximately 85% of the final dry weight of the mature seed was accumulated during the linear phase of seed growth which lasted for about 21 d. In that species, the linear growth phase started to decline at 95% of the final dry weight in all the genotypes studied.

Duration of the seed filling period is variable among grass species. The filling duration period took 17-18 d in smooth bromegrass (Bromus inermis Leyss.)(Grabe, 1956), 28 d in perennial and annual ryegrass (Lolium multiflorum Lam. (Hyde et al., 1959), 35 d in timothy, and 32 d in prairie grass (Bromus unioloides H.B.K.)(Hill and Watkin, 1975). Rate of seed filling was measured in very few of the studies of seed maturation in cool season grasses. For tall fescue reported rates were 0.0737 mg mg^{-1} day^{-1} and 0.0406 mg mg^{-1} day^{-1}, respectively at beginning and at the end of seed development with a temperature of 15 ^{o}C (Bean, 1971). In red fescue (Festuca rubra L) cv. Rubina, growth rate was 50 μg $^{o}C^{-1}$ d^{-1} and 0.4 μg $^{o}C^{-1}$ d^{-1} at those same stages of seed development (Andersen and Andersen, 1980). Rate and duration of seed filling are cultivar-related and genetically controlled in a number of species (Egli, 1981; Bruekner and Froberg, 1987).

Length, rate of seed growth and the final weight of seeds are dependent on tiller and head age. Seeds produced in early-emerged heads are the heaviest and make up the greater proportion of final yield (Stodart, 1959; Anslow, 1964; Hill and Watkin, 1975).

Moisture

The dynamics of the moisture content during maturation in seeds of cool season grasses follows a pattern that is common for other small grains and leguminous species (Grabe, 1956; Hyde et al., 1959; Lee et al., 1979; Bishnoi, 1974; Aspinall, 1975; Andersen and Andersen, 1980; Barlow et al., 1980; Nicolas et al., 1985). Seed moisture content is high during the lag phase and decreases slowly during the linear growth phase. During the third phase, after physiological seed maturity, moisture loss accelerates until it reaches an equilibrium with the relative humidity of the air .

Sofield et al. (1977b) and Barlow et al. (1980) showed that lipids are deposited at the chalazal zone of wheat (Triticum aestivum L.) seeds by the time of physiological maturity. These lipids restrict movement of water to the seeds and explains the sudden acceleration in the rate of moisture loss from the seed during ripening. Although this blocking also limits the movement of assimilates to the seed (Sofield et al., 1977b) it might not be considered to be the cause or to coincide with seed maturation. There is evidence that wheat seeds continue to grow in much smaller rate after lipids are deposited (Nicolas et al., 1984) and this indicates that the acceleration of moisture loss actually happens a day or two earlier than physiological maturity.

The process of seed abcission, a feature that indicates the low levels of domestication of pasture grasses (McWillians, 1980), might also restrict water uptake by the seeds. In perennial ryegrass, although abscission layers were present since the heading stage, the breaking of these layers only occurred 5 weeks after the anthesis (Elgersma et al, 1988). In this species there was no degradation of the abcission layer and seed sheeding was caused by a mechanical force.

Moisture content at which physiological maturity is achieved is another parameter commonly used to express the length of the seed growth period in cool season grasses. For smooth bromegrass, perennial and annual ryegrasses, timothy and prairie grass seed, physiological maturity occurred at moisture contents of 470, 380, 400, and 430 g kg^{-1}on a fresh weight basis, respectively (Grabe, 1956; Hyde et al., 1959; Hill and Watkin, 1975). The moisture content at which maximum dry weight is achieved in tall fescue seeds is approximately 500 g kg^{-1} (Bean, 1971) and 330 g kg^{-1} was the moisture reported by Hebblethwaite and Ahmed (1978) for red fescue (Festuca rubra L.). For perennial ryegrass, while Hyde et al. (1959) found seed maturity occurring at 440 g kg^{-1}, Griffiths et al. (1976) reported a moisture of 500 g kg^{-1} at maturity. Moisture content at physiological maturity in small grains varied from 380 to 500 g kg^{-1} (Bishnoi, 1974; Aspinall, 1975; Sofield et al., 1977b; Lee et al., 1979; Hanft and Wych, 1982).

Germination and Vigor

Seeds of many grasses can germinate soon after the initial phase of development and before physiological maturity or maximum seed dry weight is achieved (Hyde et al., 1959; Stoddart, 1959, 1964; Nellist and Rees, 1963, 1968; Roberts, 1969, 1971; Williams, 1972; Pegler, 1976; Hill and Watkin, 1975; Hebblethwaite and Ahmed, 1978). The timing after anthesis when maximum germination occurs, however, varies between species (Hill and Watkins, 1975; Hebblethwaite and Ahmed, 1978) and between seed heads in a population (Stoddart, 1959; Anslow, 1964). Although maximum germination is reached earlier in the seed maturation period, Grabe (1956) showed that maximum seedling vigor in smooth bromegrass was achieved only at seed physiological maturity.

Factors Affecting the Dynamics of Seed Growth

Temperature

For different species it was found that temperature affects both rate and duration of seed filling. In tall fescue, under controlled conditions, the duration of seed growth was reduced in tall fescue when the temperature increased from 15 to 25 ^{o}C (Bean, 1971). Seed relative growth rate was 0.0737 mg mg^{-1} day^{-1} for the first six days after anthesis at 15 ^{o}C. During the same period, at 20 ^{o}C, this growth rate was 0.1728 mg mg^{-1} mg^{-1}. A similar trend was observed by Andersen and Andersen (1980) for perennial ryegrass and red fescue.

Days after peak anthesis is the time unit normally used in studies of the dynamics of seed growth in cool season grasses. Since temperature affects the duration and rate of seed filling in cool season grasses (Bean, 1971; Andersen and Andersen, 1980) use of growing degree days after peak anthesis (GDD) is a better time unit for studies of seed development. This unit accounts for the daily variations in temperature and, with wheat, it stresses the differences existing between phenological events occurring in different years or between cultivars maturing in different periods of the year (Cutforth et al., 1988). There are many variations in formulas to calculate GDD and in seed development studies this unit is commonly calculated by the formula $GDD= \Sigma\{[(T_{max} + T_{min})/2]- T_b\}$ where T_b is the temperature at which seed growth stops. In wheat, base temperatures for post-anthesis events varies from 0 to 8.5 ^{o}C according to different authors (Spiertz and Vos, 1985; Keulen and Seligman, 1987; Cutforth et al., 1988).

High temperatures and drought during the post-anthesis period of wheat reduce grain yield and research has provided much information on the effects of these two variables on wheat seed development. It is likely that cool season grasses respond in the same manner to the effect of these two variables during seed development. High temperatures increase the rate of filling and reduce the duration of seed filling in wheat (Sofield et al., 1977a; Wardlaw et al., 1980; Wiegand and Cuellar, 1981). The final seed weight is normally reduced with higher temperatures because the increase in growth rate is small and insufficient to compensate for the reduction in the filling period (Tashiro and Wardlaw, 1989). The absence of expressive increases in the rate of filling is attributed to an inability of the starch synthesizing enzymes of wheat to respond to increasing temperatures (Bhullar and Jenner, 1986). On the other hand, hastening of senescence in plants (Wiegand and Cuellar, 1981) or earlier partial deposition of lipids in the chalazal zone (Nicolas et al. 1984) are accountable for the shortening of the seed growth period.

Water Stress

Effects of water stress on seed maturation of cool season grasses have not been the object of specific studies, but it was observed that the length of the seed filling period in bromegrass was reduced in a drier year (Grabe, 1956).

The effect of water stress on wheat seed development is dependent on the timing of its occurrence in relation to anthesis. When it coincides with anthesis seed set is reduced and the remaining seeds are not affected. Even small water stresses reduce length of seed growth in wheat and final seed weight when it occurs after anthesis. Rate of growth is only reduced when water stress is severe (Aspinall, 1965; Wardlaw, 1971; Nicholas et al., 1984). The capacity of accumulating carbohidrates in wheat seeds is reduced when drought is coincident with high temperatures (Nicholas et al., 1984). Water stress does not reduce the supply of carbohydrates (Wardlaw, 1971; Aggarwal and Sinha, 1984) and this earlier cessation of seed growth occurs because lipids are deposited in the chalazal zone (Wardlaw, 1971; Barlow, 1980; Nicholas et al. 1984). Results from Aspinall (1965) showed that, up to physiological maturity, the moisture content of seeds and rate of moisture loss (fresh weight basis) was not affected by water stress. Water stress, however, increased the rate of moisture loss after seed physiological maturity.

Diseases and Fungicides

There are few studies on effects of diseases and or management factors such as fungicide application on seed development in grasses. The widespread occurrence of stem rust (Puccinia graminis Pers. subsp. graminicola Urban) in the Willamette Valley was first observed in 1988 (Welty, 1989). Plants attacked during the reproductive period may show a considerable reduction of yield. Rupture of tissue, destruction of green tissue and redirection of plant assimilates are the main detrimental effects of rust in crops (Durbin, 1984; McGrath and Pennypacker, 1990; Welty, 1991) and there is evidence from wheat studies that this disease may interfere with the dynamics of seed maturation (McGrath and Pennypacker, 1991). Rust occurring during the post anthesis period of wheat reduced the length and rate of the filling period but this effect was variable according to rust intensity. Disease control with fungicides is recommended to avoid yield losses (Hampton et al., 1985; Welty, 1991). Increases in seed yield with application of fungicide were detected even in absence of disease (Hampton and Hebblethwaite, 1984; Hampton et al., 1985; Hampton, 1986) and it was attributed to both an increase in seed set and retardation of plant senescence. Propiconazole (Tilt), a triazole systemic fungicide which restricts the synthesis of ergosterol in the pathogen (Schwinn, 1983), is recommended for stem rust control in grass seed crops (Extension Services, 1989; Welty, 1991). It was shown that this fungicide can alter plant morphology and reduce gibberellic acid synthesis in plants (Buchenauer, 1987). A common effect of propiconazole in plants is the delay of senescence which can occur through reduction of chlorophyl degradation (Kettlewell and Davies, 1982), maintenance of photosynthesis rates for a longer time (Davies et al., 1984), a cytokinin-like effect (Goatley and Schmidt, 1990), and reduction of the saprophytic flora of the leaves (Riesen and Close, 1987). In perennial ryegrass, fungicide application increases seed weight and reduces floret abortion probably due to an increased leaf area duration (LAD) after anthesis (Hampton and Hebblethwaite, 1984) but an expected delay in the process of seed maturation as a result of increased LAD was not observed in perennial ryegrass (Horeman, 1989).

Harvest

Timing

When to start the harvesting operations in grass seed crops is a difficult decision seed growers experience every year. Time of harvest affects both seed yield and seed quality and a wrong decision can threaten an all-year effort towards profitability of the crop.

Two processes, weight increase in the maturing seeds and seed shedding of already mature seeds, are under way during the maturation phase of grass seed crops. They produce opposite effects on final yield and, theoretically, the optimum harvesting time occurs when effects of the two processes achieve a balance (Neelist and Rees, 1963; Williams, 1972; Andersen and Andersen, 1980). The difficulty in defining this ideal harvest time arises because both processes vary between inflorescences, spikelets and florets. Researchers have been trying to find plant physiological and morphological characteristics that would integrate this variability and provide farmers with information on the best harvesting time (Griffiths et al., 1976).

Usefulness of endosperm consistency, seed color, amount of shattering and number of days after anthesis as aides to identify the correct harvest time was reviewed by Nellist (1962). Research has shown that these morphological characteristics have variable reliability depending on species, environmental conditions and harvesting methods (Klein and Harmond, 1971; Hill and Watkin, 1975; Griffiths et al., 1976; Jensen, 1976; Andersen and Andersen, 1980).

Stoddart (1964) commented that endosperm is the largest component of the seed and that definition of harvest timing can rely on it alone. For annual and perennial ryegrass, tall and meadow fescue, cocksfoot, and timothy the best harvesting time occurred with the endosperm still soft and at the cream cheese or cheese stages (Pegler, 1976). This author pointed out that harvest at this endosperm consistency may cause mechanical damage to the seeds and suggested that adjustments in the combine would avoid such damages. Other results for perennial ryegrass, timothy and prairie grass suggested, however, that endosperm consistency may not be a reliable harvesting index (Hill and Watkin, 1975). It was observed that considerable increase in seed weight occurred after seeds had achieved the 'hard-dough' stage. Another drawback refers to the number of endosperm to be evaluated to provide good estimation of the ripeness of the seed population in a field.

Color of seeds is a common index for harvest timing in grass seed crops. Normally, a crop is considered mature for harvest when almost all seed heads have lost their greenness. For perennial ryegrass, timothy, prairie grass, and cocksfoot, however, seed maturity occurs while a great number of seeds are still green and harvests based on loss of the green color occurs after the optimum harvesting time (Hyde et al., 1959; Stoddart, 1964; Hill and Watkin, 1975). At maturity, 35% of the seed heads in perennial ryegrass, 30% in timothy and 20% in prairie grass were still green (Hill and Watkin, 1975).

Stripping ripeness, or the percentage of seeds removed by pulling and stripping seeds from seed heads, is a harvest index that evaluates the risk for seed shattering in a crop (Jensen, 1976). The optimum harvesting time occurs when most of the seeds are removed from the inflorescence and association of this index with color of the tiller improved its precision (Jensen, 1976). It is, however, an index based on evaluation of individual tillers and the sample size necessary to represent the tiller population can restrict the use of this indicator. Andersen and Andersen (1980) were able to show a high negative correlation between this index and standing seed moisture content.

Days after peak anthesis was also used as guidance for harvest timing and Roberts (1969) recommended 30 to 35 d after peak anthesis as the optimum harvesting time for S352 timothy. Use of days after peak anthesis was contested by various authors because length of seed maturation varies from year to year (Klein and Harmond, 1971; Hill and Watkin, 1975). Temperature is one of the weather variables affecting length of the seed maturation period (Bean, 1971; Andersen and Andersen, 1980) and these latter authors suggested that use of growing degree days accumulated after peak anthesis, instead of days, would be a better indicator of optimum harvest timing.

Moisture content of the standing seed crop provides a reliable indication about the harvest time for the achievement of maximum seed yields. Use of seed moisture content, alone or associated with morphological characteristics, is recommended for many grass species (Roberts, 1969, 1971; Klein and Harmond, 1971; Williams, 1972; Hill and Watkin, 1975; Griffiths et al., 1976; Pegler, 1976; Hebblethwaite and Ahmed, 1978).

The seed moisture content on a fresh weight basis indicative of optimum harvest time (harvest moisture index) varies between species and years (Hill and Watkin, 1975), with harvesting methods (Arnold and Lake, 1965 and 1966; Neelist and Rees, 1963 and 1968; Hill and Watkin, 1975), and with application of growth regulators (Wiltshire and Hebblethwaite, 1990). In one of the earliest works on the subject, Klein and Harmond (1971), although recognizing variation between years, suggested a harvest moisture index of 430 g kg^{-1} for windrowing Alta tall fescue in Oregon as an average for three years. In New Zealand, a harvest moisture index of 480 g kg^{-1} was indicated for the windrowing of tall fescue cultivar 'Grassland Roa' (Hare et al., 1990). Moisture indexes for perennial ryegrass in two consecutive years were 470 and 400 g kg^{-1}, respectively (Hill and Watkin, 1975). Andersen and Andersen (1980) presented the range of moisture indexes for maximum seed yield of a series of cool season grasses.

There are few studies comparing the moisture content at the optimum harvest date for distinct cultivars. Hill (1973) suggested that late cultivars of perennial ryegrass would be ready to harvest at higher moisture contents than earlier cultivars. Wiltshire and Hebblethwaite (1990), however, showed that the harvesting moisture index for a late cultivar of perennial ryegrass is lower than that for an early or intermediate cultivar.

Few of the studies on harvest timing had duration over two years and many were one-year studies. Conclusions in many of them were based on graphs without the use of statistical analysis of the data (Table 2.1). Despite that, across studies and species, the best harvest timing occurred at a range of moisture contents around 400 g kg^{-1}. According to Evans (1959), when environmental conditions allow the existence of a well-defined peak anthesis a corresponding harvest-timing peak for seed yield occurs. Conversely, when anthesis does not have a clear peak, there is a corresponding plateau for harvest timing to achieve maximum yields. These observations may explain some of the variation found in different studies of harvest timing. Also, many authors agreed that, unlike direct combine harvesting, the use of swathing harvesting allows optimum harvesting to occur over a wider range of seed moisture contents (Evans, 1959; Arnold and Lake, 1965; Hill and Watkin, 1975).

The possibility of predicting the best harvest time would be of value for machinery and labor management during the harvesting season on seed farms. Many authors (Klein and Harmmond, 1971; Hill, 1973; Hill and Watkin, 1975) proposed the use of "seed-drying curves" to forecast optimum harvest time in grasses and legumes. Those authors commented, however, that the influence of prevalent temperature and water stress on seed drying curves was a possible drawback for this method of forecasting. Accordingly, there is evidence from a glasshouse study that low temperature reduces the rate at which seed moisture decreases (Bean, 1971). Detailed studies in wheat have shown, however, that moisture content and water potential of seeds is not influenced by dry conditions up to physiological seed maturity (Aspinall, 1965; Wardlaw, 1971; Barlow et al., 1980). For tall fescue, as an average for three years, Klein and Harmond (1971) reported a rate of moisture loss of 25 g kg^{-1} d^{-1} in tall fescue. For perennial ryegrass that rate of moisture loss was 30 g kg^{-1} d^{-1} (Klein and Harmond, 1971) while 18 to 20 and 10 g kg^{-1} d^{-1} were reported, respectively, for perennial and tetraploid ryegrasses (Williams, 1972; Hill and Watkin, 1975). Roberts (1971) reported that rate of moisture loss for 'Sabalan' and 'Sabrina' tetraploid ryegrass was 3 g kg^{-1} d^{-1} until a moisture content of 500 g kg^{-1}. After this point, rate increased to approximately 30 g $kg^{-1}d^{-1}$. Moisture loss followed a linear trend, below a moisture content of 450 g kg^{-1} in cocksfoot seeds with rates varying from 15 to 18 g kg^{-1} d^{-1} (Arnold and Lake, 1966). For timothy, at the same stage of seed development, rate of moisture loss was around 10 g kg^{-1} d^{-1} during two years (Arnold and Lake, 1965).

Seed losses

Most of the studies on harvest timing in grasses were done in small plots and using hand harvesting (Table 1). Few authors, however, comment on the drawbacks of this methodology or on the necessary precautions to transpose their findings to mechanical harvesting at the farm level.

Natural seed shedding and losses occurring during harvesting operations are the sources of seed losses occurring in a grass seed crop (Jensen, 1976; Andersen and Andersen, 1980). These losses can be reduced by correct harvest timing and appropriate harvest method (Nellist and Rees, 1963). Klein and Harmond (1971) showed that seed growers in Oregon normally harvested their Alta tall fescue seed crops after the optimum harvesting time and obtained only 86% of the yield achievable with correct harvest timing.

Many of the studies on harvest timing in cool season grasses included measurements of seed losses (Table 1). Seed losses from natural shedding were evaluated from the inflorescence (Stoddart, 1959; Anslow, 1964; Roberts, 1969, 1971; Williams, 1972; Pegler, 1976) or collected in trays (Jensen, 1976). Only Klein et al. (1961) and Nellist and Rees (1963) reported losses occurring before and during the harvesting process. Cool season grasses start to shed at different stages of seed development. While shedding in tall fescue and ryegrass started approximately 15 - 18 d after peak anthesis, in timothy it started at 30 d after anthesis (Pegler, 1976). Results by Jensen (1976) showed that lodging and prevailing wind speed were factors causing variation in seed shedding between years in meadow fescue. In tetrapoid ryegrass cv. Sabel shedding started at 550 g kg^{-1} and rate of shedding increased sharply when the seed moisture content dropped below 440 g kg^{-1} (Williams, 1972). For another cultivar of tetraploid ryegrass, shedding started when moisture content was 410 g kg^{-1} (Roberts, 1971). For tall fescue, the total losses after harvest were around 38 and 34% of the potential yield for direct combining and windrow combine, respectively. Pre-harvest shedding and cutterbar shattering were the main sources of losses with direct combining while losses from windrow shattering and pick up shattering where the most important with windrow combining (Klein et al., 1961). Losses from swath-harvested plots increased from 9.6 to 24.8% of the potential yield during seed ripening in cocksfoot. For direct-harvesting those losses increased from 2.7 to 14% (Nellist and Rees, 1963).

Table 2.1. Summary of the methodologies used in studies of harvest timing in cool season grasses.

Author	Statistical Analysis/	Duration years	Species/ varieties	Plot size	Harvest method	Index	Losses
Anslow, 1964	no	1	ryegrass	0.7 m^2	manual	color, moisture shedding,	yes
Arnold and Lake, 1965	yes	2	cocksfoot	-	manual	moisture	no
Arnorld and Lake,1966	yes	2	timothy	6 m^2	mechanic	moisture	yes
Hebblethwaite and Ahmed,1978		1	various	2.6m2	manual	moisture	no
Hill and Watkin,1975	yes	2	various	2.7m2	manual	moisture	no
Jensen, 1976	no	4	meadow fescue/1	samples	-	various	yes
Klein and Harmond , 1971	no	3	many spp	-	combine	moisture	yes
Pegler, 1976	no	2	many spp	sheaves	manual	moisture, endosperm	yes
Roberts, 1969	no	1	timothy/11	sheaves	manual	moisture, days	yes
Roberts, 1971	no	1	ryegrass/2	sheaves	manual	moisture , days	yes
Roberts, 1977	yes	1	ryegrass/7	-	manual	moisture	no
Nellist and Rees , 1963	yes	1	ryegrass/1	145 m^2	combine	moisture	no
Nellist and Rees, 1963	yes	1	cocksfoot/1	400m^2	combine	days	yes
Stoddart, 1964	no	2	various	sheaves	manual	carbohidrate	no
Stoddart, 1959	yes	2	timothy/3	10 m^2	manual	color	no
Stoddart, 1959	yes	2	timothy/3	0.3 m	manual	color	yes
Willians, 1972	yes	1	ryegrass	90 m^2	combine	moisture	yes
Wiltshire and Hebblethwaite, 1990	yes	1	ryegrass/3	1.5 to 4.4m^2	manual	moisture	no

CHAPTER 3

QUANTITATIVE AND VISUAL DETERMINATION OF PEAK ANTHESIS IN TURF-TYPE TALL FESCUE SEED CROPS

Abstract

Peak anthesis is a useful phenological reference point in grass seed production and research. However, daily anthesis is weather-dependent and it is difficult to identify seasonal peak anthesis by visual observation. This study was conducted to investigate daily and seasonal flowering patterns of tall fescue (Festuca arundinacea Schreb.) in relation to weather variables and to improve the accuracy of visual determination of peak anthesis. The study was conducted in 1991 and 1992 with 'Chesapeake', an early-maturing cultivar and 'Emperor', a late cultivar. Hourly and daily flowering intensity were estimated by the amount of pollen collected by Burkard spore samplers. Two visual methods of estimating peak anthesis were compared with the pollen-collection method. Averaged over days, daily peak anthesis occurred at 1400 h in 1991 and 1600 in 1992 in both cultivars. Daily flowering intensity was affected by maximum temperature and radiation occurring on the same day but not by weather conditions occurring during the 5 previous days. Daily flowering intensity in 1991 fluctuated with variation in daily temperatures and there was no single day of peak anthesis. Rather, there were several peaks, making a visual estimate of peak anthesis impossible. With less variation in daily maximum temperatures in 1992, the day of peak anthesis was evident and visual estimation was accurate. Calculation of mid-anthesis may be a preferable alternative to visual determination of peak anthesis since it is less subjective and requires fewer trips

to the field. In years with an undisturbed bell-shaped seasonal flowering pattern, mid-anthesis coincided with seasonal peak anthesis.

Introduction

Date of flowering, normally defined as the day of "peak anthesis" or the day on which the greatest proportion of flowers is in anthesis, is a useful phenological reference point in grass seed production and research. Flowering in a grass seed crop, however, occurs over several days because of variation in flowering time between individual plants, fertile tillers, and florets within the inflorescences. Also, with anemophylous grasses, the timing of anthesis is weather-dependent and flowers normally open when weather is favorable for pollen dispersal by the wind (Dafni, 1992; Faegri and Pijl, 1979). These factors make it difficult to identify peak anthesis by visual observation.

The need to increase crossing efficiency in breeding projects motivated the initial studies of flowering patterns in cool-season grasses. Flowering was studied through direct counting of opened flowers (Emecz, 1962), or through counting of pollen grains impacting on exposed microscope slides or glass tubes (Jones and Newell, 1946; Dotzenko and Stegmeier, 1959; Jensen, 1976). These methods are labor-intensive and limited the duration and sampling frequency in those studies. Although pollen measurements were sometimes limited to a few days of single seasons, researchers agreed that weather conditions affected the timing and quantity of opened flowers and that temperature was the most influential of the weather parameters. The development of practical methods for determination of seasonal peak anthesis in grass seed crops, however, received little attention.

A greater knowledge of factors affecting daily and seasonal flowering patterns in cool-season grasses can be acquired with automatic sampling equipment to quantify daily pollen shedding. This information can then be used to reduce subjectivity in visual determination of peak anthesis. The objective of this work was to employ a continuous spore sampler to study daily and seasonal flowering patterns of tall fescue in relation to weather variables. This information can be applied to improve the accuracy of visual determination of peak anthesis in turf-type tall fescue.

Materials and Methods

The flowering patterns of turf-type tall fescue were studied during 1991 and 1992 at the Oregon State University Hyslop Crop Science Field Laboratory near Corvallis, OR. Stands of Chesapeake, an early-maturing cultivar, and Emperor, a late cultivar, were established in September 1989, in 45-cm rows. Management and harvesting procedures followed practices for tall fescue seed production in the Willamette Valley.

Hourly and daily flowering intensity were estimated by the amount of pollen collected by Burkard spore samplers (Burkard Manufacturing Co., Woodcock Hill Industrial Estate, Rickmansworth Hertfordshire WD3 1P, England). The samplers were positioned just above the seed heads in the center of 15 by 30 m areas of each variety. This spore trap is a device that, using a battery-powered vacuum pump, continuously samples the amount of particles suspended in the air (Ogden et al., 1974). Pollen grains were collected on a tape which covered a drum rotating in front of the air-input orifice. The tape was coated with a mixture of petroleum gel and paraffin 9:1 w/w dissolved in toluene. In the laboratory, the tape was aligned over a template and cut into 48-mm segments corresponding to each day. The daily segments of tape were marked with a razor blade at 2-mm intervals corresponding to each hour of the day. After staining (Lacy and Pontius, 1983), tape segments were mounted on a microscope slide and pollen grains were counted under 100x magnification. Pollen counts were made in 0.3-mm^2 areas on the central longitudinal axis of the hourly tape segments.

Two visual methods of estimating peak anthesis were compared with the Burkard. Observations of opened florets were made each afternoon during the flowering period, and a subjective determination was made regarding the day with the greatest flowering intensity. In the second method, the beginning and ending dates of anthesis were recorded, and the mid-point of the flowering period was determined.

Daily maximum and minimum temperatures and daily total radiation data were collected at the Hyslop Farm Weather Station near the experimental site. Sensitivity of daily flowering to temperature and total radiation during the day of flowering and during the five previous days was evaluated by the method developed by Steiner and Opoku-Boateng (1991). Flowering intensities during the final one third to one fourth of the flowering periods were not included in the sensitivity study because flowering intensity decreased then irrespective of weather conditions. Sensitivity was considered to occur when the coefficient of determination of the associations of flowering intensity with the weather parameters had a probability of ≤ 0.01. Regression equations associating daily flowering intensity and daily maximum temperature or radiation were compared after variances were tested for homogeneity according to procedures described by Neter et al. (1989).

Results and Discussion

Daily Flowering Patterns

Daily flowering patterns for the two cultivars formed a bell-shaped distribution slightly skewed towards the afternoon hours with an acute peak for Chesapeake in 1992 and for Emperor in both years (Fig 3.1.). Heavy lodging of Chesapeake in 1991 probably trapped pollen inside the plant canopy, which could explain the lower amount of pollen collected that year. Chesapeake also lodged during 1992, although less than in 1991. For both cultivars during the two years, the amount of pollen produced during the 3-h period around the daily peak anthesis was correlated ($r = > 0.90$, $p < 0.01$) with the total pollen produced that day. Consequently, the precision of visual assessment of seasonal peak anthesis depends on how well field visits coincide with daily peak anthesis.

Although pollen grains were present in samples from the night hours, flowering in tall fescue is diurnal. Daily flowering started around 0800 h and increased gradually to an afternoon peak which approximately coincided with the daily maximum temperature. After this peak, pollen shedding decreased sharply with little or none occurring after 2000 h (Fig 3.1.). Averaged over days, daily peak anthesis occurred at 1400 h in 1991 and 1600 h in 1992 in both cultivars. Other reports of daily peak anthesis in tall fescue are 1430 h (Jones and Newell, 1946; Jones and Brown, 1951) and 1508 h (Emecz, 1962).

The general pattern of afternoon flowering, however, did not apply to the initial days of the flowering period. At the start of the flowering period in 1991, daily peak anthesis in Chesapeake was observed during the morning . The daily flowering pattern at beginning of flowering in Chesapeake in 1992, and in Emperor in both years, had a small peak in the morning and a main peak in the afternoon. This agrees with the findings of Emecz (1962) that a third of the flowers of S 170 tall fescue flowering in June opened during the morning, while morning flowering was not observed during July.

Daily weather conditions, however, were the main cause of variations in the timing of daily peak anthesis. The earlier peak anthesis in 1991 probably was related to an earlier occurrence of the daily maximum temperature in that year. Unfavorably cool temperatures frequently delayed peak anthesis until late afternoon or prevented anthesis altogether. Intensity of flowering the previous day also influenced the timing of peak flowering on the following day. Flowering generally occurred earlier in the day following a period with low flowering intensity. Night temperature did not influence the timing of peak anthesis, although Hill (1971) reported that daily peak anthesis in ryegrass (Lolium perenne L.) occurred earlier in days following nights with temperatures above 10 ^{o}C.

Seasonal Flowering Patterns

Tall fescue flowering in 1992 occurred under warmer and sunnier conditions than in 1991. For Chesapeake and Emperor, respectively, daily maximum temperatures were 4.5 and 3.4 ^{o}C higher during 1992 (Table 3.1), and mean total daily radiation was greater in 1992 because of fewer overcast days.

The flowering period of both cultivars was shorter and 3 wk earlier in 1992 (Fig 3.2.). Chesapeake started to flower on 3 June 1991 and on 15 May 1992 with flowering lasting for 27 and 15 d. In Emperor, a late variety, flowering began on 17 June 1991 and lasted for 20 d. For the same cultivar, flowering started on 23 May 1992 and continued for 18 d. Bean (1971) also found that higher temperatures shortened the flowering period of tall fescue under glasshouse conditions.

During 1991, days of intense flowering were followed by days with reduced or no flowering, and a distinct peak anthesis did not occur in either cultivar (Fig 3.2.). Jensen (1976) indicated that a plateau, instead of a peak, also characterized the flowering pattern of meadow fescue (Festuca pratensis Huds.) in years with dull and cold conditions. A bell shaped pattern with a definite peak was apparent for Chesapeake and Emperor during 1992, although both cultivars had a few days with reduced flowering intensities. Similar bell-shaped flowering patterns were observed in other cool and warm-season grasses (Jones and Newell, 1946).

Higher daily maximum temperatures enhanced daily intensity of flowering (Fig 3.4.). Flowering intensity in any day was generally sensitive to the maximum temperature of that day but not to maximum temperatures during any of the five previous days (Fig 3.3.). An exception was Chesapeake in 1992, when flowering intensity was also sensitive to the maximum temperatures 1 and 4 d before (Fig 3.3.). Emecz (1962) classified tall fescue as a "quick-staminating" species. These species do not need long exposure to optimum conditions for the opening of flowers, and the flowering process is mainly responsive to concurrent weather conditions.

Daily intensity of flowering was not affected by daily minimum temperature (Fig 3.3.).

These results support general statements that flowering in anemophylous plants is weather-dependent and anthers dehisce only when conditions are warm, dry and favorable for wind dispersion of the pollen grains (Faegri and Pijl, 1979). Studies with other grasses have shown that temperature is the most influential weather variable affecting flowering patterns of grasses (Jones and Newell, 1946; Dotzenko and Stegmeier, 1959).

Daily flowering intensity increased with increases in daily radiation (Fig 3.5.). Flowering intensity responded to the concurrent radiation in 1991 but not in 1992 (Fig 3.3.). Except for one instance, there was no evident flowering response to radiation level during the previous 5-d period. In most cases, therefore, flowering intensity responded similarly to temperature and radiation. Emecz, (1962) commented that weather parameters such as radiation and air relative humidity influence the temperature occurring at the plant level and this last parameter alone can be used to study the influence of weather parameters on grass flowering. This was verified in the present study where daily maximum temperature and radiation during the flowering period were correlated ($r=0.70$, $p<0.01$).

For Emperor in 1992, daily maximum temperatures and radiation were quite uniform, and this had a uniform day-to-day influence on flowering (Fig 3.3.). This promoted the establishment of a distinct single date of peak anthesis which did not occur when temperatures were more variable (Fig 3.2.).

The intercepts on the X axis in figures 4 and 5 provided an estimate of the daily temperature and radiation threshold values below which flowering does not occur. For Chesapeake, these threshold temperatures were 13.7 ^{o}C and 14.4 ^{o}C during 1991 and 1992, respectively. For Emperor, 12.6 ^{o}C was the threshold temperature in 1991 (Fig 3.4.). These regression equations were compared and no differences were found between years for Chesapeake or between the two cultivars in 1991 and it suggests a common threshold temperature of around 13.5 ^{o}C. In Nebraska, flowering in tall fescue was reduced by temperatures of 14.5 to 15.7 ^{o}C (Jones and Newell, 1946) and those authors suggested an optimum temperature of 25.7 ^{o}C for the flowering of this species. Such a quadratic association was not observed in the range of temperature and radiation values experienced by Chesapeake and Emperor.

The minimum temperature required for flowering in S 170 tall fescue in England was 17 ^{o}C (Emecz, 1962). During 1991, radiation threshold values for Chesapeake and Emperor were 5.90 and 5.27 M J m^{-2}, respectively (Fig 3.5.). Lack of variance homogeneity did not allow the comparison of regression equations fitting the radiation data.

Estimation of Seasonal Peak Anthesis

The Burkard sampler provided reliable measurements of hourly pollen shedding. This allowed indirect estimates of both daily and seasonal flowering patterns and permitted identification of the day of peak anthesis when it existed (Fig 3.2.). Cost, requirement of a power source, and the time consumed in preparation of tapes and counting pollen restricts the use of Burkard samplers in commercial seed production. The Burkard, however, provides precise data for pollination studies and can serve as a standard reference for developing visual methods of estimating peak anthesis.

According to pollen measurements, there was no single day of peak anthesis in 1991 (Fig 3.2.). Rather, there were several peaks, making a visual estimate of peak anthesis impossible. An estimation of peak anthesis is difficult and can be misleading because of the tendency of recognizing one of the various peaks as the seasonal peak anthesis. For instance, during the highly variable flowering period of Chesapeake in 1991, peak anthesis was visually estimated to occur on day 161 (Table 3.2). Fig 3.2. shows that flowering intensity on that day was high, but not the peak of the season. With a more bell-shaped distribution of flowering and pollen dispersal in 1992, peak anthesis was accurately estimated by visual observation (Table 3.2).

Calculation of the midpoint of the flowering period appears to be a promising alternative to peak anthesis as a descriptor of flowering time in tall fescue. With a bell-shaped distribution in 1992, mid-anthesis was nearly identical to the peak anthesis determined with the Burkard sampler (Table 3.2). With erratic flowering in 1991, mid-anthesis was 4 to 5 d later than the visual estimate of peak anthesis. By using mid-anthesis as a base point, approximately the same amount of pollination occurs before and after this date, whether there is a definite peak anthesis or not. Determination of mid-anthesis is less subjective than peak anthesis. It is also more practical because fewer trips to the field are required and observations do not have to be made during daily peak anthesis.

Conclusions

The Burkard spore sampler provided reliable data on daily and seasonal pollination patterns in tall fescue. According to pollen counts, daily peak anthesis occurred between 1400 and 1600 h. Weather fluctuations may cause daily fluctuations in pollen density, resulting in no evident time of seasonal peak anthesis. In such years, visual determinations of peak anthesis are not possible. Calculation of mid-anthesis may be a preferable alternative to determination of peak anthesis since it is less subjective and requires fewer trips to the field. In years with an undisturbed bell-shaped seasonal flowering pattern, mid-anthesis coincides with seasonal peak anthesis. In years without a distinct peak anthesis, mid-anthesis is still a useful guideline since it is approximately the midpoint of the pollination period.

Table 3.1. Mean daily temperatures and radiation during the flowering period of Chesapeake and Emperor tall fescue.

Year	Mean daily temperatures: Maximum	Mean daily temperatures: Minimum	Mean daily radiation
	°C	°C	M J m^{-2}
	Chesapeake		
1991	19.8 (15.6)†	8.7 (11.7)	15.99 (22.7)
1992	24.3 (14.4)	8.2 (10.0)	19.68 (16.8)
	Emperor		
1991	22.6 (21.7)	10.2 (7.2)	18.94 (27.2)
1992	26.0 (9.4)	8.8 (7.2)	23.49 (27.5)

† Numbers in parentheses are the range of variation between days.

Table 3.2. Estimators of peak anthesis in Chesapeake and Emperor tall fescue.

Year	Flowering period: Beginning	Flowering period: Ending	Estimators of peak anthesis: Mid-anthesis	Estimators of peak anthesis: Peak pollen density	Estimators of peak anthesis: Visual
	Day of year				
	Chesapeake				
1991	153	180	166	-†	161
1992	135	150	142	143	144
	Emperor				
1991	167	187	177	-†	173
1992	143	161	152	152	152

† No evident peak

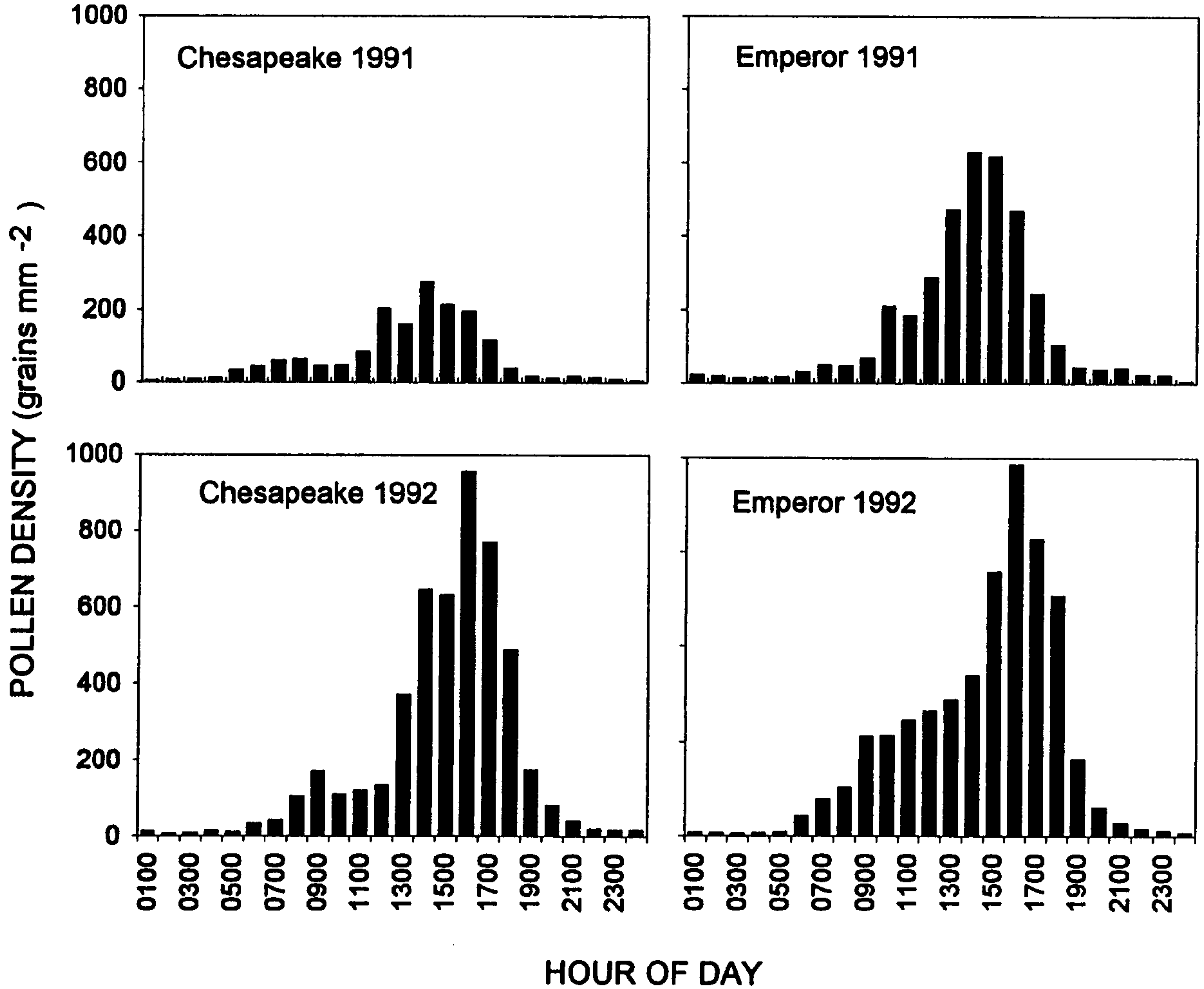

Fig. 3. 1. Mean daily flowering patterns in Chesapeake and Emperor tall fescue.

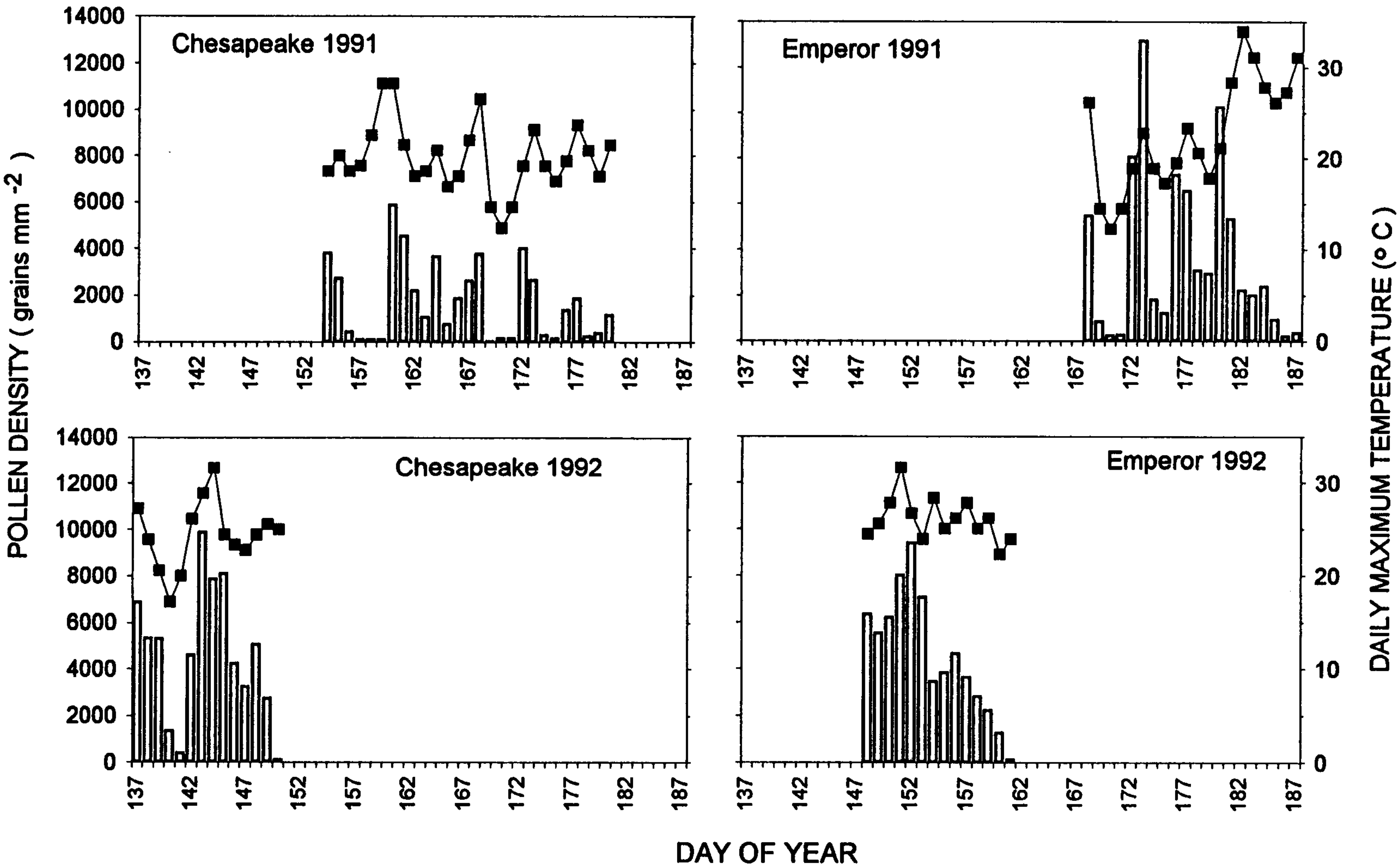

Fig. 3.2. Daily maximum temperature and seasonal flowering patterns in Chesapeake and Emperor tall fescue. (■ = temperature)

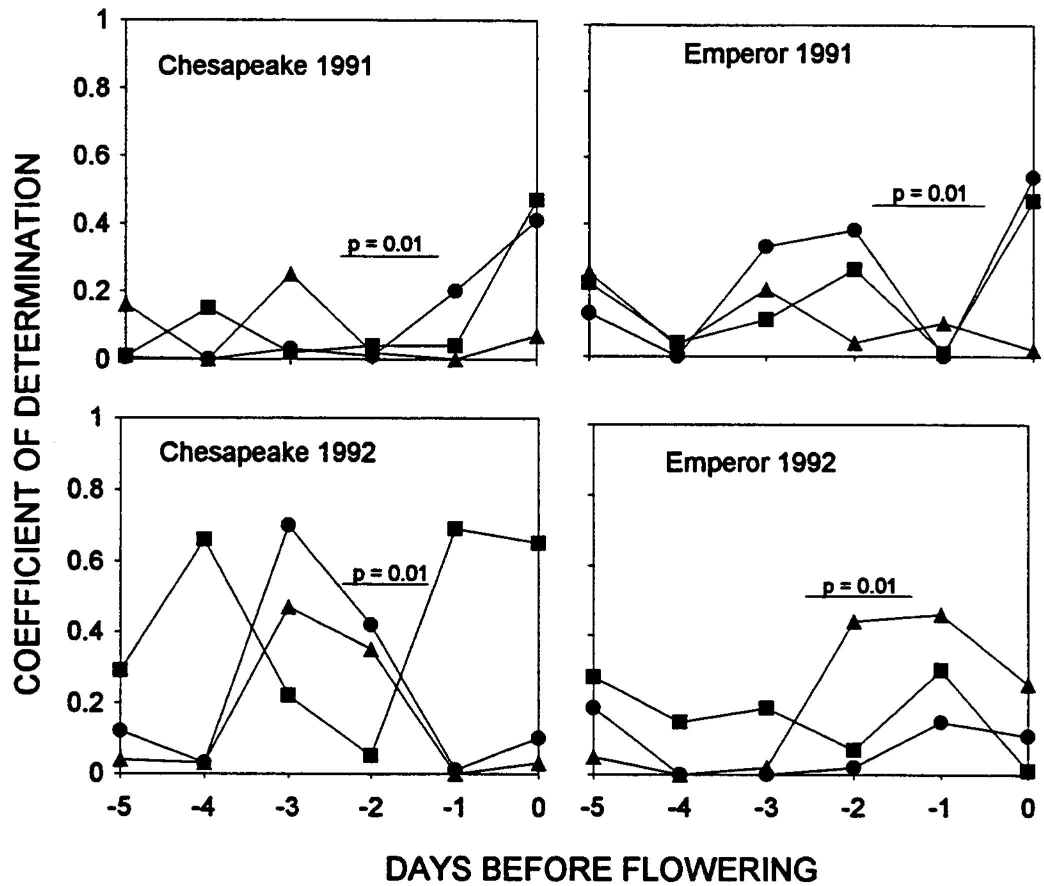

Fig. 3.3. Effect of daily maximum and minimum temperatures and radiation from -5 days to the day of flowering on the daily flowering intensity as measured by the linear coefficient of determination. (■ daily maximum temperature; ▲ daily minimum temperature; ● radiation; horizontal line represents the 0.01 probability level for the coefficients of determination).

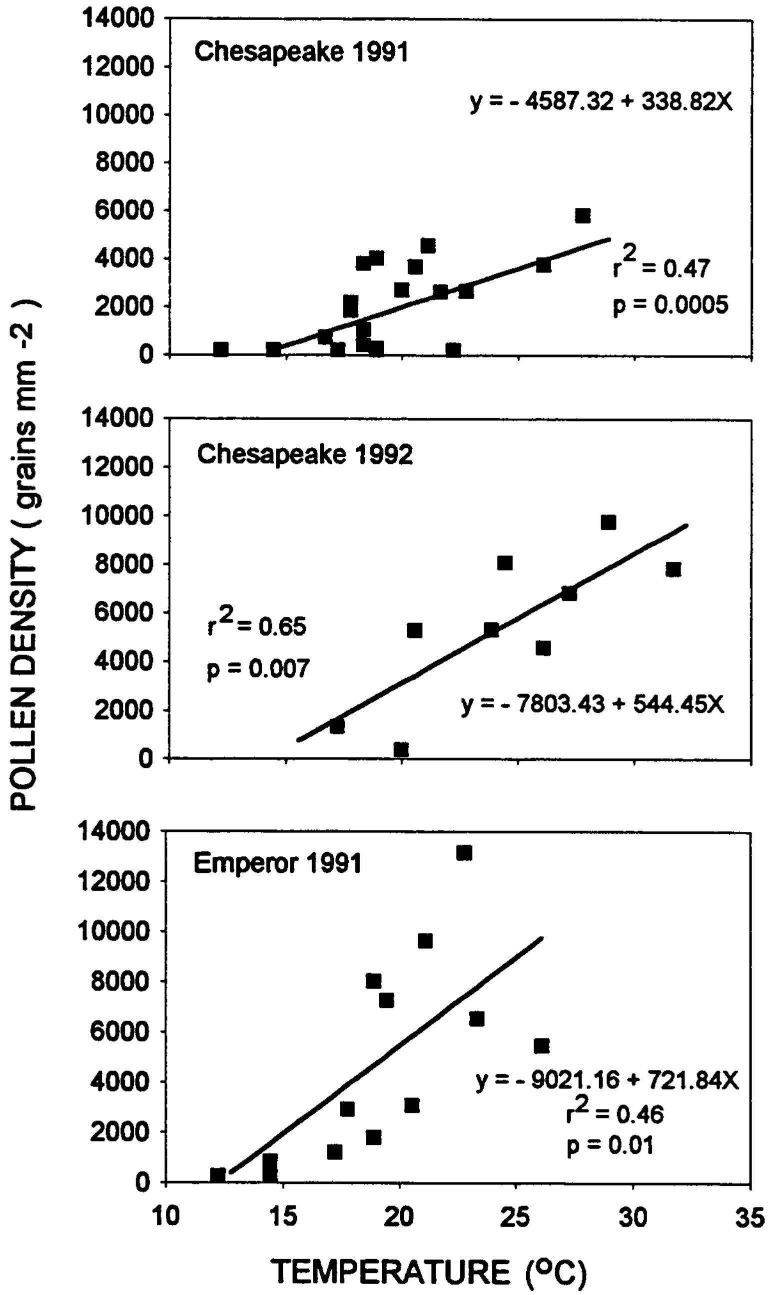

Fig. 3.4. Association between daily maximum temperature and daily flowering intensity in tall fescue.

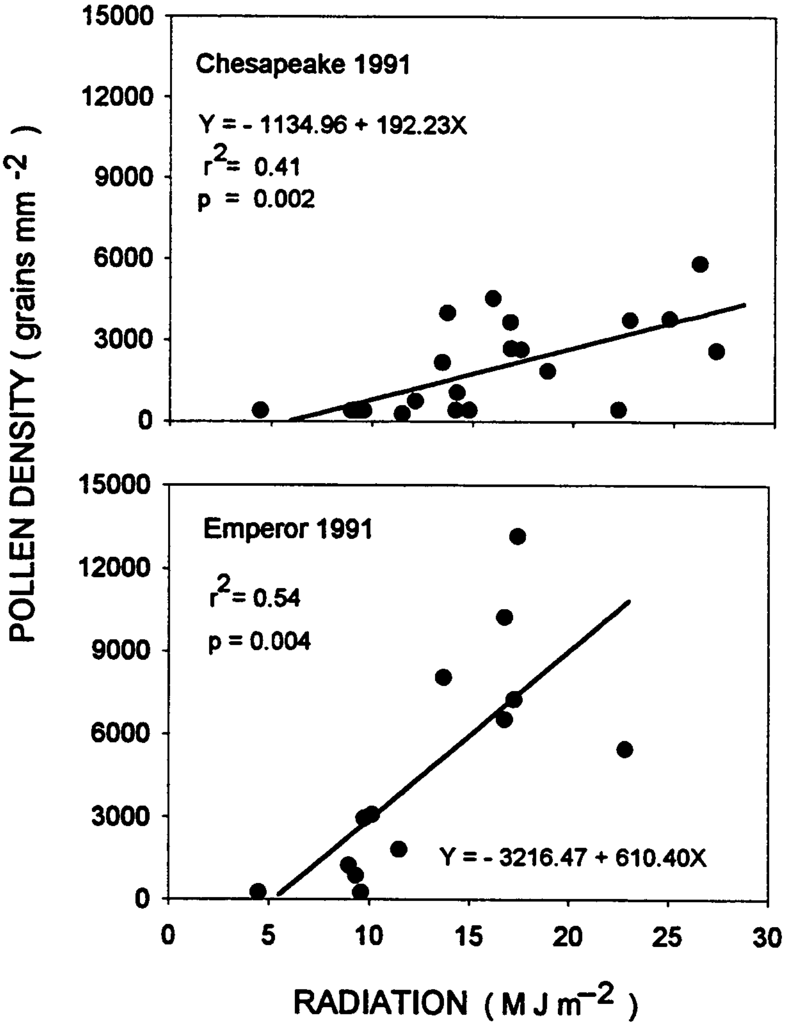

Fig. 3.5. Association between daily radiation and daily flowering intensity in tall fescue.

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CHAPTER 4

TALL FESCUE SEED MATURATION IN RESPONSE TO PROPICONAZOLE AND STEM RUST

Abstract

An understanding of factors affecting seed development and maturation is important for determining optimum harvesting time for grass seed crops. The objectives of this work were to investigate the normal course of seed development and to determine the effects of propiconazole (1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl-methyl]-1H-1.2.4-triazole) and stem rust (Puccinia graminis Peers subsp. graminicola Urban) on seed maturation of tall fescue (Festuca arundinacea Schreb.). Two experiments were conducted with 'Chesapeake' (early flowering) and 'Emperor' (late flowering) turf-type tall fescue. Both cultivars are susceptible to stem rust. Seed development in untreated plots was compared to that in plots treated with propiconazole to control stem rust. In Exp. 1, stem rust did not develop on untreated plots in either of two years and propiconazole had no effect on seed maturation of either cultivar. Physiological maturity (PM) occurred at moisture contents of 400 to 480 g kg^{-1}. In Exp. 2, extensive stem rust infection occurred in both cultivars. Since propiconazole had no effect on seed development in Exp. 1, it could be assumed that any differences in seed development in Exp. 2 were due to rust and not propiconazole. For Chesapeake, rust occurred during anthesis, reducing seed growth rate and slightly lengthening the filling duration, resulting in seeds that were 8.5% lighter. In Emperor, rust occurred 16 d before anthesis and reduced filling duration by 3.9 days (63 GDD) causing seeds to be 20 % lighter in the

control plots. Accumulated GDD between anthesis and PM was not consistent; however, the dynamics of moisture change during seed maturation were less affected by rust or propiconazole.

Introduction

An understanding of factors affecting seed development and maturation is important for determining optimum harvesting time for grass seed crops. Most studies of grass seed development have concentrated on measuring rates of moisture loss and increases in viability and dry weight over time. The moisture content at which maximum dry weight occurs is a commonly used index of physiological maturity (PM). PM was achieved 17-18 d after anthesis in smooth bromegrass (Bromus inermis Leyss.)(Grabe, 1956), 28 d in perennial ryegrass (Lolium perenne L.)and annual ryegrass (Lolium multiflorum Lam.)(Hyde et al., 1959), 35 d in timothy (Phleum pratense L.) and 32 d in prairie grass (Bromus unioloides H.B.K.)(Hill and Watkin, 1975). For the same species, PM occurred at moisture contents of 470, 440, 380, 400, and 430 g kg^{-1} , respectively.

Plant disease and chemicals used for disease control have the potential to affect seed growth and maturation. With the outbreak of stem rust (Puccinia graminis Peers subsp. graminicola Urban) in tall fescue seed crops in 1988 (Welty, 1989), the fungicide propiconazole became one of the preferred options for disease control to maintain seed yields. This systemic fungicide belongs to the triazole group which inhibits ergosterol synthesis in the pathogen (Schwinn, 1983), can reduce gibberellic acid synthesis in plants, and can affect plant morphology (Buchenauer, 1987). Propiconazole retards chlorophyll degradation, stimulates photosynthesis and delays leaf senescence (Goatley and Schmidt, 1990; Davies et al., 1984; Riesen and Close, 1987). There have been suggestions from grass seed growers that propiconazole delays seed maturity in grasses.

The objectives of this work were to investigate the normal course of seed development and maturation in tall fescue and to determine the effects of propiconazole and stem rust on seed maturation. An additional objective was to determine the relationship of growing degree days (GDD) to the rate of seed maturation.

Materials and Methods

Two experiments were conducted at the Oregon State University Hyslop Crop Science Field Laboratory near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixerolls). Chesapeake (early flowering) and Emperor (late flowering) cultivars of turf-type tall fescue were included in both experiments. Both cultivars are susceptible to stem rust. Exp. 1 was conducted in 1991 and 1992 on plots established on areas that were fall seeded in 1989 and from which a seed crop was harvested in 1990. Exp. 2 was conducted in plots seeded 30 Aug. 1991 approximately 100 m from Exp. 1. General practices for establishment, weed control, fertilization and post-harvest management followed the recommendations for tall fescue seed production in the region. Experimental procedures were similar in both experiments.

Meteorological Data

Meteorological data were collected at the Hyslop Farm weather station near the experimental site. The number of growing degree days (GDD) was calculated by the formula $GDD = \Sigma\{[(T_{max} + T_{min})/2] - T_{base}\}$. T_{base} was considered to be 3 ^{o}C.

Plant Development

Starting on day 53 in 1991(23 February) and on day 3 in 1992(03 January), 10 of the largest tillers in a 10-cm sample of row were inspected weekly under magnification to determine the occurrence of the double-ridge stage of flower initiation. Date of initiation was considered to be when 80% of the tillers were in the double-ridge stage. Peak anthesis was considered to occur at the mid point of the flowering period (Chapter 3).

Application of Propiconazole

Treatments were propiconazole at a rate of 0.183 kg a.i. ha^{-1} (0.440 L ha^{-1}) and controls without fungicide. The fungicide was applied with a back pack sprayer delivering a volume of 450 L ha^{-1}. The experimental design was a completely randomized design with four replications. Plot size was 2.7 by 3.0 m (six rows 3 m long).

In Exp. 1, fungicide was applied on 28 May and 24 June 1991. At the first application, Chesapeake was starting to flower and Emperor was at the heading stage. During the second application Chesapeake had reached the seed filling phase while Emperor was at peak flowering. In 1992, the first fungicide treatment was applied on 21 April with Chesapeake at the boot stage and Emperor at the stem elongation stage. The second application was made on 11 May when Chesapeake was at beginning anthesis and Emperor was heading.

In Exp. 2, propiconazole was applied three times during the spring of 1992. The first two applications were made at the same time as those in Exp. 1. During the first application Chesapeake was starting to head and Emperor was at the stem elongation phase. The second application was made at the flowering stage for Chesapeake and immediately before flowering in Emperor. A third application was made on 27 May at which time Chesapeake was at the post-anthesis phase while Emperor was flowering.

Rust Ratings

Stem rust severity on the flag leaf and inflorescence was evaluated using a modified Cobb scale (Peterson et al., 1948). Severity ratings were made at 10 to 14-d intervals on two tillers in each of the four central rows of each plot. The flag leaf blade in Chesapeake senesced very rapidly after anthesis so rust severity for this cultivar was measured on the flag leaf sheath. Rust evaluations on the inflorescence were made on a 10-cm segment of the culm below the first branch of the inflorescence. The rust severity ratings were used to construct disease progress curves over the seed development period. The area under the disease progress curve (ADPC) for rust severity was calculated by the procedures of Shaner and Finney (1977) and analyzed by a t-test.

The percentage of the flag leaf with dead tissue was also estimated on the same tillers used for rust severity evaluation. The ADPC formula for rust severity was used to determine the area of the flag leaf with dead tissue.

Seed development

Seed samples for weight and moisture determination were taken every 1 or 2 d during 1991 and every 2 or 3 d in 1992 starting soon after completion of anthesis. Contamination from dew was avoided and moisture was not determined on rainy days. Seeds were stripped at random from inflorescences in the central four rows leaving a border of 0.5 m at each end of the plots. Stripped seeds were collected in closed plastic containers and taken to the laboratory within 15 min for processing. Seed moisture was calculated on a fresh weight basis after drying 1 h in a forced-air oven at 130 ^{o}C (ISTA, 1993).

Four samples of 100 seeds each were weighed for determination of dry seed weight. At the time of weighing, seeds contained about 100 g kg^{-1}

moisture. Seed weights before the point of seed moisture loss acceleration (MLA) were regressed on GDD to estimate the seed growth rate during the linear phase of seed growth. These regressions were compared by the method of Neter et al. (1989). The intercept of this line estimated the glume weight. Final seed weight was obtained by averaging seed weights after MLA. Seed filling duration in GDD was estimated by subtracting weight of the glumes from final seed weight and dividing the result by the seed filling rate. Filling duration in days was calculated by dividing the filling duration in GDD by the daily rates of GDD accumulation.

A logistic model (Darroch and Baker, 1990) was used to fit the seed growth data for each treatment. The independent variable was GDD accumulated after peak anthesis. Models fitting each treatment were compared using the general linear method after the assumption of variance homogeneity was tested with an F test at the 0.05 probability level (Neter et al., 1989). In the absence of differences, the data were pooled for comparisons between years and for description of the dynamics of seed maturation.

Results and Discussion

Experiment 1

The growing season in 1992 was generally drier and warmer than in 1991, imposing some moisture stress on the late-maturing Emperor in 1992 (Table 4.1). Precipitation during reproductive development of the plants in 1992 was 37 and 143 mm less for Chesapeake and Emperor, respectively. Maximum and minimum temperatures from January through May were respectively 3.5 and 1.6 ^{o}C higher during 1992 than 1991. Because of their different maturity dates, the daily average temperature during the post-anthesis period in 1992 was 1.8 ^{o}C higher for Chesapeake, but 2.7 ^{o}C lower for Emperor than in 1991.

Rust Development and Flag Leaf Senescence. Stem rust did not develop on untreated plots in either year, but natural senescence led to development of dead tissue on the flag leaves. Treatment with propiconazole in 1992 resulted in smaller areas of dead tissue in Emperor after PM as indicated by smaller ADPC measurements (Table 4.2). It is likely that the drier spring in 1992 led to premature leaf senescence and enhanced the anti-senescence effect of propiconazole in the late-maturing Emperor. This delay in leaf senescence, however, did not affect Emperor seed maturation. Propiconazole had no effect on flag leaf senescence in either cultivar in 1991 or in Chesapeake in 1992.

Reproductive Development in Response to Propiconazole. The timing of floral initiation and anthesis varied widely between years and cultivars (Table 4.4). The growing points of Chesapeake underwent floral initiation by 24 Jan. 1992, 28 d earlier than in 1991. Initiation occurred in Emperor by 02 Mar. 1992, 20 d earlier than in 1991. The earlier initiation in 1992 is attributed to the 4.1 ^{o}C higher temperature in January. Mid-anthesis in Chesapeake occurred 118 d after initiation in 1992 and 115 d in 1991. The corresponding times for Emperor were 89 and 96 d. The flowering periods for Chesapeake were 28 d in 1991 and 18 d in 1992, while the corresponding periods for Emperor were 20 d in 1991 and 16 d in 1992.

Seed moisture content decreased gradually during the seed filling period (Fig. 1). An abrupt moisture loss acceleration (MLA) occurred at moisture contents of 480 to 500 g kg^{-1} in Chesapeake and 490 to 520 g kg^{-1} in Emperor. Studies with other cool-season grasses (Grabe, 1956; Hill and Watkin, 1975; Andersen and Andersen, 1980), and with small grains such as wheat (Triticum aestivum L. em. Thell), and barley (Hordeum vulgare L.) (Sofield et al., 1977; Aspinall, 1975; Barlow et al., 1980) have also shown that water loss from maturing seeds follows a characteristic pattern in which MLA occurs near PM. Development of an abscission layer, which in perennial ryegrass occurs concurrently with attainment of maximum seed weight (Elgersma et al., 1988) is a likely cause for the interruption of water flow to the seeds resulting in MLA . In wheat, Sofield et al. (1977) attributed MLA to lipid deposition in the chalazal zone, which blocks the route of water and assimilates to the seed. In the present study, MLA was considered a good indication of the end of the linear seed growth period in the calculation of the rate and duration of tall fescue seed filling (Table 4.4).

Application of propiconazole did not affect seed development of either cultivar in either year (Table 4.3 and 4.4). Therefore, seed development data were pooled for plotting Fig. 4.1 and for comparison between years and cultivars. Lack of homogeneity in the variances for the models fitting the pooled seed growth data for Chesapeake prevented comparisons between years.

However, models fitting Emperor seed maturation differed between years (Table 4.3).

For Emperor the filling period was 92 GDD (5 d) shorter while the filling rate was 0.0013 mg GDD^{-1} higher in 1992. The higher rate of seed filling resulted in similar seed weights both years (Table 4.4). The drought during 1992 probably caused the shorter filling period in Emperor. The seed maturation period in smooth bromegrass was also reduced in a drier year (Grabe, 1956), and water stress reduced the filling period of wheat (Nicolas et al., 1985; Barlow, 1980). The higher rate of seed filling was probably related to the lower average daily temperature of 16 ^{o}C during the seed maturation of Emperor in 1992 (Table 4.1). This temperature was lower than that observed during 1991, and close to the temperature of 15 ^{o}C found by Bean (1971) to be conducive to higher seed growth rates and production of heavier seeds in tall fescue. Dry seed weight increased in small increments after MLA, with small fluctuations and no obvious termination point (Fig. 4.1). Final seed weight, therefore, was calculated to be the average of the dry seed weights after MLA. The day on which this average weight was reached was considered to be the date of physiological maturity (PM). This date was consistently about 2 d after MLA at moisture contents of 400 to 480 g kg^{-1}. A period of 3 d existed between MLA and PM in wheat (Nicolas et al., 1985), further confirming the close association between the timing of MLA and PM in seeds. PM in Chesapeake occurred 20 d after mid-anthesis in 1992 and 23 d in 1991. For Emperor, the corresponding times were 18 and 23 d. The moisture contents and days at which PM occurred (Table 4.4) are comparable to the values observed in other species of cool-season grasses (Grabe, 1956; Hyde et al., 1959; Hill and Watkin, 1975; Andersen and Andersen, 1980).

These variations in timing of reproductive stages led to Chesapeake seed maturing 29 d earlier in 1992 than in 1991, and Emperor maturing 32 d earlier in 1992. Earlier maturity in Chesapeake in 1992 was predominantly due to earlier initiation, while earlier maturity in Emperor was due to earlier initiation, earlier peak anthesis and a shorter filling period.

The heat units accumulated between mid-anthesis and MLA in Chesapeake were 290 and 270 GDD in 1991 and 1992, respectively (Fig. 4.1). For the same cultivar, 305 and 302 GDD were accumulated from mid-anthesis until PM. This narrow range in GDD occurred under favorable moisture and temperature conditions. However, MLA in Emperor occurred 334 and 243 GDD after mid-anthesis (Fig. 4.1) while PM occurred after 361 and 269 GDD (Table 4.4). This lack of consistency in GDD between years for Emperor may have been related to the moisture stress that occurred in 1992 with this late-maturing cultivar (Table 4.1). The variation in GDD required for maturation of Emperor would reject the suggestion that GDD could be a more consistent index of seed maturity than days after anthesis. However, additional trials may indicate that GDD could be combined with moisture content and days after anthesis as an index of PM.

Experiment 2

Disease Development. Extensive stem rust infection occurred in both cultivars. The ADPC values for rust severity in control plots during seed development were 1099 and 412 on the flag leaves of Emperor and Chesapeake, respectively. The ADPCs for the inflorescence were 939 and 241 for Emperor and Chesapeake (Table 4.5). The higher ADPC values for Emperor indicate that rust infection was much more severe than on Chesapeake.

Rust occurred at different phenological stages in the two cultivars because of differences in the timing of reproductive development. Rust was detected at beginning of anthesis in Chesapeake, but the incidence remained low during the following 10 d. With Emperor, rust occurred 16 d before anthesis and attacked the inflorescence more extensively than in Chesapeake. By day 163 (14 June), all the tissue in the flag leaf of Emperor was dead, due to rust or natural senescence.

Propiconazole provided good rust protection in the sprayed plots. By the end of the seed development period, areas of dead tissue in the flag leaves of both cultivars were much samller in treated plots (Table 4.5).

The severity of stem rust in Exp. 2 in 1992 was unexpected since rust was absent that year in Exp. 1 which was located only 100 m distant. While Exp. 1 was conducted on a third-year stand and Exp. 2 on a first-year stand, there is no evidence to indicate that age of stand is a determinant of rust susceptibility. However, for experimental purposes, this was a fortunate circumstance. The lack of rust in Exp. 1 made it possible to study the single effect of propiconazole on seed development. The presence of rust in Exp. 2 made it possible to study the single effect of stem rust, knowing that propiconazole did not affect seed development.

Effect of Stem Rust on Seed Development. Without rust in Exp. 1, propiconazole did not affect seed development. Therefore, it could be assumed that any differences in seed development in Exp. 2 were due to rust and not propiconazole.

For Chesapeake, rust reduced seed growth rate by 25% and lengthened the seed filling duration by 9 GDD (approximately 1 d), resulting in seeds that were 8.5% lighter (Table 4.6). In Emperor, although seeds from non-sprayed plots were lighter throughout the sampling period (Fig. 4.2), seed growth rates were similar to those in treated plots (Table 4.6). However, as filling duration was reduced by 62 GDD (3.9 d), seeds were 20% lighter in the control plots (Table 4.6, Fig. 4.2). These observations lead to the conclusion that seed maturity, rather than being delayed by propiconazole, may be hastened by stem rust infection.

The timing of stem rust attack in relation to anthesis probably conditioned the variable response of the seed growth parameters to the disease in the two cultivars. It is known from research in small grains that rust disease competes for assimilates, reduces photosynthesis and photosynthetic area, and increases water stress through water losses from the damaged tissue (Durbin, 1984; McGrath and Pennypacker, 1990). The two main sources of assimilates for the seed in cool season grasses are the inflorescence (Marshall, 1985) and to a lesser extent the flag leaf (Clemence and Hebblethwaite, 1984). As both sources of assimilates were attacked in the two cultivars, it can be assumed that the disease reduced assimilate supply to the seeds and increased the water stress that plants suffered in 1992. It is possible to speculate that, since rust occurred after anthesis in Chesapeake, it did not affect seed set, but reduced assimilate supply and increased competition between the developing seeds. This resulted in a smaller seed growth rate and a longer seed filling duration. With Emperor, the disease occurred 2 wk before anthesis, probably reducing seed set in the control plots but allowing the remaining seeds, although smaller, to grow at a rate similar to that observed in the disease-protected plots. Water stress associated with disease accelerated plant senescence, reduced filling duration, and resulted in lighter seeds in the non-protected plots.

Rust had little effect on seed moisture relationships during maturation. As in Exp. 1, MLA occurred at seed moisture contents of approximately 500 g kg^{-1}, with PM occurring about 2 d later at 40 to 60 g kg^{-1} lower moisture levels (Table 4.6).

Conclusions

In the absence of stem rust, propiconazole did not affect seed maturation of the two cultivars of tall fescue. Propiconazole may reduce the rate of leaf senescence, and the greener plants can lead to misinterpretation of the degree of ripeness of the seed crop. The effect of stem rust on the development of tall fescue seeds was dependent on the timing of disease occurrence in relation to plant phenological development. When it occurred by the beginning of anthesis, as with the early-maturing Chesapeake, rust reduced seed growth rate, extended filling duration, and caused a small decrease in final seed weight. When stem rust infection started before anthesis, as in the late-maturing Emperor, it did not affect seed growth rate but reduced filling duration and final seed weight. GDD may be a useful supplement to days after peak anthesis and seed moisture content as indexes of seed PM.

Table 4.1. Weather data during reproductive development of Chesapeake and Emperor tall fescue.

Cultivar	Year	Rainfall‡	Daily temperature† Average maximum	Average minimum	Daily average	Average daily GDD
		mm	°C			
			Experiment 1			
Chesapeake	1991	342	22.5	9.7	16.1	13.5
	1992	305	26.7	9.2	17.9	15.4
Emperor	1991	243	26.6	10.5	18.5	15.8
	1992	130	22.9	8.7	15.8	15.0
			Experiment 2			
Chesapeake	1992	341	25.6	8.6	17.1	14.0
Emperor	1992	130	25.0	9.1	17.0	15.8

† From mid-anthesis to seed maturation.
‡ From initiation to seed maturation.

Table 4.2. Effect of propiconazole on area under the disease progress curve (ADPC) for dead tissue in the flag leaf of Chesapeake and Emperor tall fescue in 1992.

Cultivar	Day of year	ADPC Propiconazole	Control	
Chesapeake	163	1173	1285	ns
Emperor	173	1515	1838	*

* Significant at the 0.05 probability level according to t-test.

Table 4.3. F test for comparisons between models fitting treatments and years.

Variety	Year	Comparisons	n1	n2	F calc.	F test
		Experiment 1				
Chesapeake	1991	Tilt X Control	92	92	0.822	NS
Chesapeake	1992	Tilt X Control	48	48	0.417	NS
Emperor	1991	Tilt X Control	52	52	0.382	NS
Emperor	1992	Tilt X Control	48	48	0.227	NS
Chesapeake	-	1991 X 1992	184	96	†	
Emperor	-	1991 X 1992	104	96	101.708	**
		Experiment 2				
Chesapeake	-	Tilt X Control	52	52	12.390	**
Emperor	-	Tilt X Control	56	56	283.630	**

** Significant at the 0.01 probability level.

† Not compared because of non-homogeneity of variances.

Table 4.4. Reproductive development and response of seed growth parameters to propiconazole and yearly conditions in Chesapeake and Emperor tall fescue in Exp. 1.

Cultivar	Year	Treatment	Initiation	Anthesis First	Anthesis Mid	Final seed weight	Filling rate	Filling duration		Moisture content at PM§	Moisture content at MLA¶
			—— Day of year		——	mg	mg GDD^{-1}	GDD	d	—— g kg^{-1}	——
Chesapeake	1991	Propiconazole	52	153	167	2.484a†	0.0048a‡	302	22.4	450	480
	1991	Control	52	153	167	2.473a	0.0047a	308	22.8	440	480
	1991	Pooled#	52	153	167	2.477	0.0047	305	22.6	440	480
Chesapeake	1992	Propiconazole	24	133	142	2.316a	0.0053a	296	19.2	470	500
	1992	Control	24	133	142	2.317a	0.0051a	307	19.9	450	500
	1992	Pooled	24	133	142	2.316	0.0052	302	19.6	460	500
Emperor	1991	Propiconazole	81	167	177	2.175a	0.0036a	360	22.7	400	480
	1991	Control	81	167	177	2.161a	0.0034a	361	22.8	400	500
	1991	Pooled	81	167	177	2.168A	0.0035B	361	22.8	400	490
Emperor	1992	Propiconazole	61	142	150	2.197a	0.0044a	281	18.7	480	530
	1992	Control	61	142	150	2.199a	0.0052a	259	17.3	470	520
	1992	Pooled	61	142	150	2.198A	0.0048A	269	17.9	480	520

† Final seed weight followed by different letters in each cultivar are different according to a t-test ($p \leq 0.05$). Capital letters refer to comparisons between years for pooled data.

‡ Rates followed by different letters in each cultivar are different according to an F-test ($p \leq 0.01$). Capital letters refer to comparisons between years for pooled data.

§ PM = Physiological maturity.

¶ MLA= Moisture loss acceleration.

Propiconazole and control treatments did not differ and data were pooled.

Table 4.5. Area under the disease progress curve (ADPC) for stem rust disease and dead tissue in Chesapeake and Emperor tall fescue.

			ADPC		
Cultivar	Treatment	Day of year	Flag leaf†	Inflorescence	Dead tissue in flag leaf †
Chesapeake	Propiconazole	159	51	9	22
	Control		412	241	319
			*	*	*
Emperor	Propiconazole	163	116	208	548
	Control		1099	939	938
			*	*	*

* Significant at the 0.05 probability level according to t-test.

† Rust severity and area of dead tissue evaluated on the flag leaf sheath of Chesapeake and on the flag leaf blade of Emperor.

Table 4.6. Reproductive development and response of seed growth parameters to stem rust disease in Chesapeake and Emperor tall fescue.

Cultivar	Year	Treatment	Initiation	Anthesis First	Anthesis Mid	Final seed weight	Filling rate	Filling duration		Moisture content at PM§	Moisture content at MLA¶
			—— Day of year ——			mg	mg GDD^{-1}	GDD	d	—— g kg^{-1} ——	
Chesapeake	1992	Propiconazole	37	126	136	2.307 a†	0.0051 a‡	317	22.6	480	520
	1992	Control	37	126	126	2.110 b	0.0038 b	326	23.3	450	510
Emperor	1992	Propiconazole	61	138	148	2.126 a	0.0039 a	337	21.3	450	510
	1992	Control	61	138	148	1.687 b	0.0040 a	275	17.4	480	530

† Final seed weight followed by different letters in each cultivar are different according to a t-test ($p \leq 0.05$).

‡ Rates followed by different letters in each cultivar are different according to a F-test ($p \leq 0.01$).

§ PM = Physiological maturity.

¶ MLA= Moisture loss acceleration.

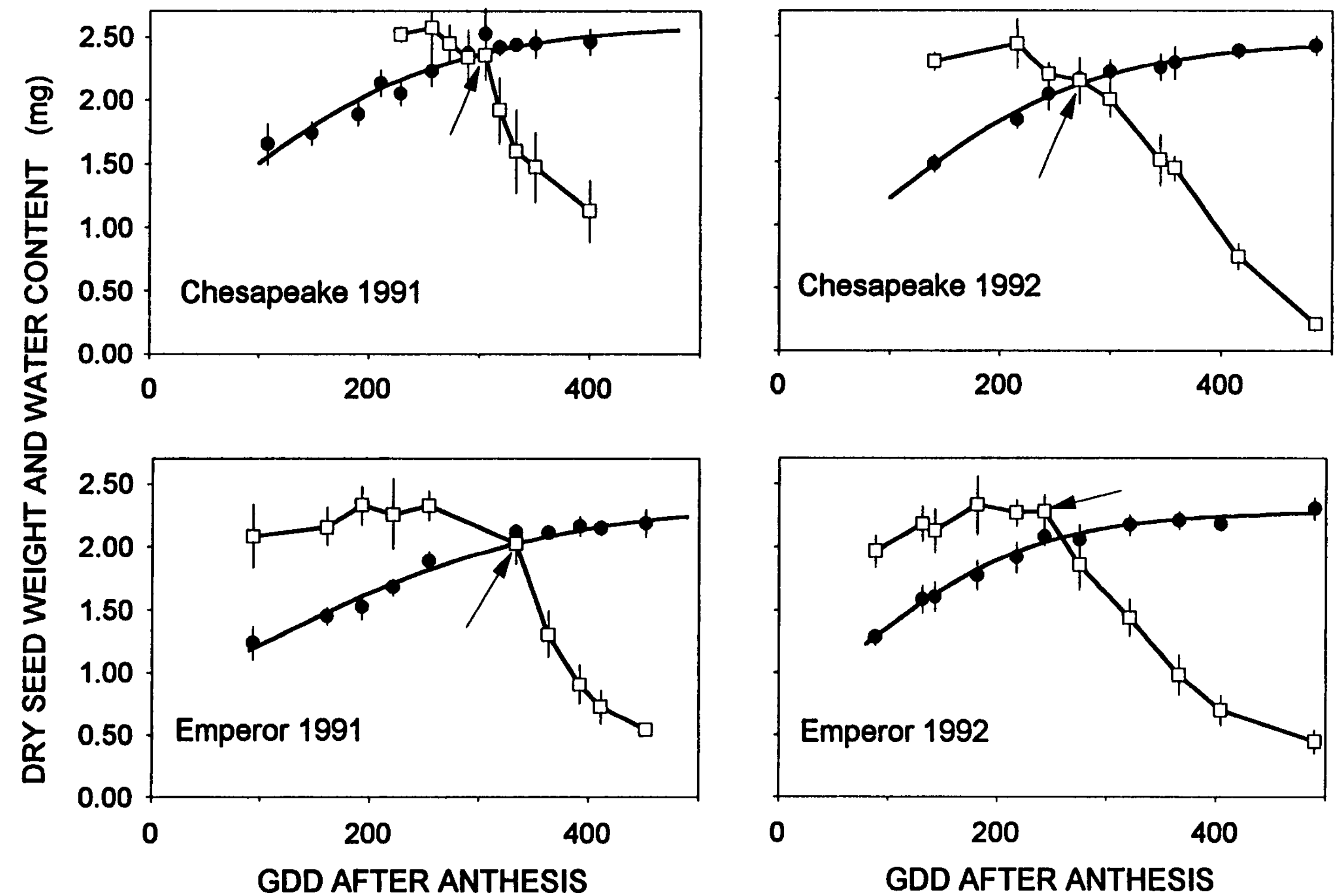

Fig. 4.1. Relationship between dry seed weight (●), water content (□), and GDD in Chesapeake and Emperor tall fescue in Exp. 1. (Arrows indicate beginning of moisture loss acceleration; data from propiconazole-treated and untreated plots are pooled; vertical lines indicate the mean standard error, n=8. For some data points the standard error was smaller than the symbol.)

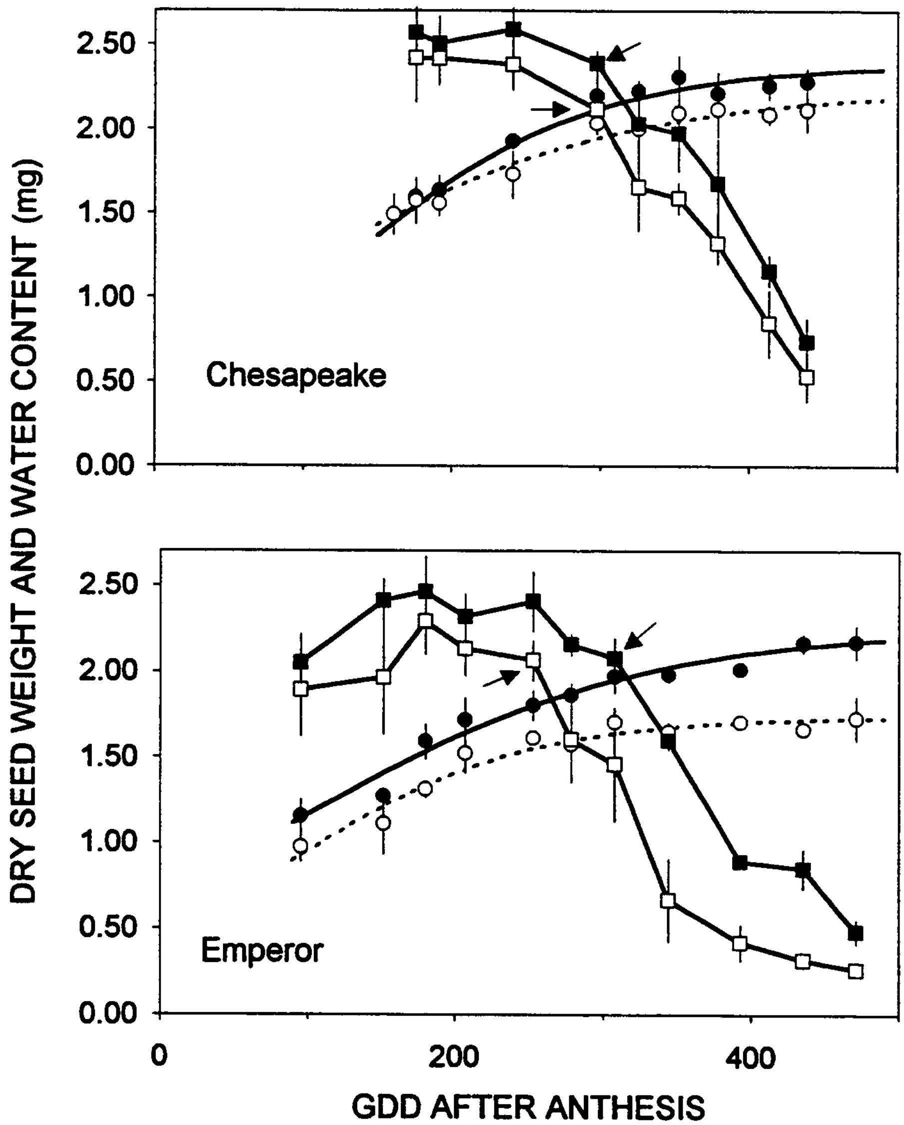

Fig. 4.2. Effect of propiconazole on dry seed weight (● ○) and water content (■ □) during maturation in Chesapeake and Emperor tall fescue in Exp. 2. (Propiconazole= full symbols; control= empty symbols; arrows indicate beginning of moisture loss acceleration; vertical lines indicate the mean standard error, n=4. For some data points the standard error was smaller than the symbol.)

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CHAPTER 5

SEED MATURATION AND HARVEST TIMING IN TURF-TYPE TALL FESCUE

Abstract

The lack of uniformity in tiller and inflorescence development in a tall fescue (Festuca arundinacea Schreb.) seed crop leads to asynchronous seed maturation and difficulty in determining optimum harvest timing. This study was conducted to determine the seed moisture content at windrowing for achieving maximum seed yield in turf-type cultivars of tall fescue with differing maturity dates. The experiments were conducted in 1990, 1991, and 1992 with 'Chesapeake, 'Bonanza', and 'Emperor' tall fescue, which are early, medium and late cultivars, respectively. Seed moisture content was determined daily. A plot-size windrower and a combine with a special pick-up attachment were used for windrowing and threshing the plots. Plots were harvested six times at successively lower moisture contents. Natural seed shedding and total seed losses were evaluated for each harvest. Seed moisture loss during maturation occurred in two phases. Average daily moisture losses were 11.5 g kg^{-1} in phase 1 and 34 to 52 g kg^{-1} in phase 2. Maximum yields were obtained by windrowing at moisture contents of 350 to 410 g kg^{-1}. In this range, maximum dry seed weight and germination percentage were achieved and natural seed shedding was minimal. When harvested at approximately 400 g kg^{-1} moisture content, average harvest losses were 27 and 12% of the yield in 1991 and 1992, respectively. The number of growing degree days (GDD) accumulated after peak anthesis was not consistent enough to be used as a harvest index in place of moisture content or days after anthesis.

Introduction

The lack of uniformity in tiller and inflorescence development in a tall fescue seed crop leads to asynchronous seed maturation and difficulty in determining optimum harvest time. Before optimum harvest time, seed quality is low and maximum yield is not achieved because of the high proportion of immature and low-weight seeds. After the optimum harvest time, seed losses from natural shedding and harvest shattering lower yields (Griffiths et al., 1976; Williams, 1972; Andersen and Andersen, 1980; Nellist and Rees, 1963; Klein et al., 1961). These losses add to the soil seed bank and increase the population of volunteer plants in the following seed crop. Therefore, correct harvest timing not only provides maximum yield but also is an effective, cheap, and environmentally safe method of reducing volunteer plants in succeeding crops.

Seed moisture content has been recommended as an index of optimum harvest time in cool season grasses (Klein and Harmond, 1971; Hill and Watkin, 1975). Unlike other seed harvest indexes, instrumentation is available for seed moisture measurement and seed moisture integrates in one figure the average condition of a population of seeds in different stages of maturation. Precision of this harvest index, however, can be improved by concomitant use of other seed maturity indicators such as endosperm consistency, color of seed heads and glumes, and degree of seed shattering (Griffiths et al., 1976; Roberts, 1969 and 1971; Williams, 1972; Pegler, 1976; Hebblethwaite and Ahmed, 1978; Andersen and Andersen, 1980). For 'Alta', an early-flowering forage-type tall fescue, on-farm research showed that, when averaged over 3 years, maximum seed yields were obtained with harvests at a moisture index of 430 g kg^{-1} (Klein and Harmond, 1971). In New Zealand, harvest at a seed moisture content of 480 g kg^{-1} is indicated for 'Grassland Roa' tall fescue (Hare et al., 1990). It is not known whether these moisture indexes also apply to turf-type cultivars of tall fescue, especially those with later maturity dates. Other researchers have indicated that optimum harvest time occurs over a range of moisture contents instead of at a sharply defined single value (Andersen and Andersen, 1980). For instance, harvesting in the range of 400 to 500 g $kg^{-1}$was recommended for achievement of maximum yields in perennial ryegrass (Lolium perenne L.), while the range of moisture contents for maximum yields of red fescue (Festuca rubra L.) was 300 to 400 g kg^{-1}. Harvest timing based on number of days after anthesis, although an easy method and commonly used, is not reliable (Hill and Watkin, 1975). An alternative time-related index, based on growing degree days (GDD) accumulated after anthesis, was suggested by Andersen and Andersen (1980). GDD would account for the influence daily temperature has on post-anthesis events in grasses.

Moisture decrease during seed maturation follows a characteristic pattern and use of "drying curves" allows the forecasting of optimum harvesting time according to seed moisture content (Hill and Watkin, 1975; Klein and Harmond, 1971; Andersen and Andersen, 1980). Development of cultivar-specific moisture-loss curves could allow seed growers to more accurately predict optimum harvest time.

Many harvest-timing studies in grasses did not consider the effects of cultivar and yearly climate variations. Conclusions were often based on hand-harvested experiments that neglected machine-shatter losses. The objectives of this study were to examine patterns of moisture loss in maturing seed crops, and to determine the seed moisture content at windrowing for achieving maximum seed yield in cultivars of tall fescue with differing maturity dates. The use of GDD accumulated after mid-anthesis as a harvest index was also studied.

Materials and Methods

The experiment was carried out at the Oregon State University Hyslop Crop Science Field Laboratory near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixerolls). Chesapeake, Bonanza, and Emperor, which are respectively early, medium, and late-flowering cultivars of turf-type tall fescue, were planted in September 1989 in rows 0.45 m apart. An application of 280 kg ha^{-1} of 16-20-0 was made during seeding and the area was top dressed with 45 kg ha^{-1} of N as urea on March 1990. Straw was eliminated from the harvested plots on 5 Sep. 1990 with two passes of a propane burner, and 280 kg ha^{-1} of 16-20-0 was applied on 1 Oct. 1990. Nitrogen (45 kg ha^{-1}) was applied as urea on 8 Mar. 1991. After the second year's harvest, a crew-cutter was used to chop and remove the straw from the plots on 9 Sep. 1991. The plots were top dressed with 280 kg ha^{-1} of 16-20-0 on 31 Sep. 1991 and with two applications of N (25 kg ha^{-1} each) as urea on 20 Feb. and 18 Mar. 1992.

Propiconazole (1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl-methyl]-1H-1.2.4-triazole) applications during spring controlled stem rust (Puccinia graminis Peers subsp. graminicola Urban) while weeds and volunteer plants were controlled with herbicides. Application of both chemicals followed recommendations for tall fescue seed crops in the Willamette Valley.

Meteorological data were collected at the Hyslop Farm Weather Station, near the experimental site. GDD was calculated by the formula $GDD = \Sigma\{[(Tmax + Tmin)/2]-Tb\}$ where Tmax and Tmin are, respectively, daily maximum and minimum temperature and Tb is a base temperature of 3 ^{o}C.

The experimental design was a randomized complete block with four replications for each cultivar. Plots were 15 m long by 2.25 m wide (5 rows 15 m long) and the central three rows were harvested. Treatments were six harvest times at successively lower seed moisture contents.

Seed moisture content was determined (ISTA, 1993) on a daily basis beginning several days before maturation. A plot-size windrower and a combine with special pick-up attachment were used for cutting and threshing the plots. The windrower had a 1.5-m cutter bar with a draper that placed the windrowed material in a 0.5 to 0.7-m windrow placed in the middle of the plot (Ehrensing et al., 1991a). The combine was a Wintersteiger Nursery Master Elite (Wintersteiger America, Lincoln, NE) with a pick-up attachment for threshing small plot windrows. This pick-up was adapted from a commercially available unit (Sund Manufacturing, Newberg, ND) used with full-size combines . A rubber draper with flexible rubber fingers lifts and deposits the windrows on the combine platform (Ehrensing et al., 1991b). Threshing occurred approximately 10 to 15 d after windrowing. Seeds were cleaned in air-screen machines to a final purity of over 95 % before weighing for yield. Before seeds were cleaned, a sample was taken for seed weight determination. Germination tests (ISTA, 1993) were conducted approximately 6 mo after harvesting.

Total seed losses were evaluated after the 1991 and 1992 harvests by vacuuming shattered seed from the ground in three 0.25 by 1.5 m areas in each plot.

Natural seed shedding was also evaluated in 1991 and 1992. Seeds were collected in 16 trays (0.16 by 0.24 m) placed in the inter-row space beneath the canopy of adjacent plots of Chesapeake and Emperor. These plots were of the same age, seeding pattern and management as the harvested plots. The trays were positioned at the beginning of the seed maturation period. A wide-mesh wire net, bent to form a tunnel over the trays, avoided seed shattering during emptying and repositioning of the trays. Seeds from the trays and from the vacuumed samples were cleaned with table-top air-screen machines and seed blowers.

Chesapeake plots lodged before anthesis during each of the three years. During the 1991 and 1992 seasons, soon after lodging and before anthesis, lodged plants of this cultivar were aligned parallel to the rows with a fork. Lodging also occurred to a lesser degree with Bonanza and Emperor in 1990 and 1991. In these cultivars lodging occurred after anthesis, and the risk of causing seed shattering prevented organizing the lodged plants over the rows. Lodging was minimal in Bonanza and did not occur in Emperor during 1992, the drier of the three years. During 1991, and to a much smaller degree during 1992, Chesapeake also lodged in the area where natural seed shedding was measured. In this area, Emperor did not lodge either year.

Germination data were transformed with an arcsin transformation for analysis of variance. Spiline models (Freund and Littell, 1991) were used to represent the association between seed moisture content and GDD accumulated after peak anthesis. Peak anthesis was considered to occur at the mid-point of the flowering period. Prospective knots for changing of the slope of the regression lines were selected from charts. The knot producing the regression equation with the smallest mean square error was selected. For Bonanza and Emperor, a period with rain prevented moisture sampling for approximately 5 d in 1991 and the knot was estimated using the SAS procedure spiline models with unknown knots (Freund and Littell, 1991). Daily rates of moisture loss were calculated by multiplying the average daily GDD accumulation by the rate of moisture loss per GDD obtained from each of the regression equations in the spiline model. For each cultivar, after homogeneity of variances was tested with an F test ($P \leq 0.05$), the regression equations fitting each of the two phases of the drying process were compared between years following the method proposed by

Neter et al. (1989). Yield data were regressed on seed moisture content and on GDD after mid-anthesis using quadratic polynomials. For those years in which the quadratic association between yield and standing seed moisture content was significant ($P \leq 0.10$), the seed moisture content for maximum yields was calculated by the formula $M.C._{(max.\ yield)} = -2a/b$ where a and b are parameters from the quadratic equation (Neter et al., 1989).

Results and Discussion

Weather Data

Climate conditions during 1990 and 1991 were favorable for seed production in tall fescue (Table 1). During 1992, however, precipitation was below normal for most of the reproductive period and seed maturation occurred under water stress, especially for the late cultivar Emperor. Higher temperatures during the inductive period of 1992 advanced maturity of the cultivars by approximately 1 mo, and flowering occurred under cooler temperatures than in the previous years.

Pattern of Seed Moisture Decrease During Seed Maturation

A two-phase pattern of moisture loss during seed maturation and ripening occurred in each cultivar each year (Fig. 1). The first phase (P1) began shortly after anthesis at moisture levels above 600 g kg^{-1}. Seeds lost moisture at a fairly constant 0.8 g kg^{-1} GDD^{-1} or 11.5 g kg^{-1} d^{-1} until reaching a level of approximately 500 g kg^{-1}. The second phase (P2) started after this point with rates of moisture decrease three to four times higher than those during P1 (Table 2).

For P1, the rates of moisture decrease did not differ between years (Table 2). In spite of the drier conditions, the rates of moisture loss observed in 1992 during P1 in Bonanza and Emperor tended to be smaller than in the previous years. Average daily GDD during P1 in 1992 were the smallest for Bonanza and Emperor and it is likely that these cooler conditions account for the lower rates of moisture decrease observed in that year. In glasshouse studies of tall fescue seed maturation, the rates of moisture decrease were slower at 15 ^{o}C than at 20 or 25 ^{o}C (Bean, 1971).

Daily rates of moisture decrease during P2 varied between 2.5 to 3.1 g kg^{-1} GDD^{-1} or from 34 to 49 g kg^{-1} d^{-1} for Chesapeake and Emperor. For Bonanza, rates were higher and varied from 42 to 52 g kg^{-1} d^{-1} (Table 3). The rate of moisture decrease per GDD during P2 was highest during 1991 ($p \leq 0.05$) for Chesapeake. For the other two cultivars there was no difference between years in the rate of moisture decrease during this phase.

For each of the cultivars, the beginning of P2 occurred at moisture contents around 500 g kg^{-1} in two out of three years (Table 3). In 1992, for Chesapeake, and in 1990, for Bonanza, this starting point occurred at 460 g kg^{-1}. P2 started at 490 g kg^{-1} in Emperor during 1990.

During the three years, P2 started after 288 to 299 GDD were accumulated after peak anthesis for Chesapeake. With Bonanza, despite a higher value in 1991, the GDD accumulation before P2 showed little variation between 1990 and 1992 and was fairly constant at values around 309 GDD. The number of GDD accumulated before P2 was variable between years for Emperor. With this cultivar the number of GDD accumulated until the starting of P2 was smaller in 1992 probably because water stress reduced the period of seed maturation. During the 3 years, the number of days from peak anthesis until P2 varied from 19 to 21 d in Chesapeake, and from 21 to 24 d in Bonanza. For Emperor, there were 20 d from anthesis to P2 during 1990 and 1991 and 17 d during 1992. During 1991, a rainy spell during the seed development period prevented moisture samplings and reduced the number of samplings around P2 for Bonanza and Emperor (Fig. 1). In spite of that, across cultivars and years, seed moisture content appeared to show less variability than GDD and days after anthesis for identifying the beginning of P2. GDD and days after anthesis were a reliable indicator of P2 only for the cultivar Chesapeake.

A two-phase pattern of moisture decrease during seed development was observed in other cool season grasses (Grabe, 1956; Hill and Watkin, 1975; Andersen and Andersen, 1980) and in wheat (Sofield et al., 1977). The higher rates of moisture decrease during P2 indicates that the seed is no longer receiving water from the plant and has entered a process of drying. Deposition of lipids in the chalazal zone, as observed in wheat (Sofield et al., 1977) and/or the formation of an abscission layer, which occurs concurrently with physiological seed maturity (McWilliam, 1980; Elgersma et al., 1988), restricts seed water uptake and causes acceleration of moisture loss.

Several authors have suggested the use of 'drying curves' for forecasting the best harvest time in cool season grasses (Klein and Harmond, 1971; Hill and Watkin, 1977; Andersen and Andersen, 1980). These authors, however, assumed a uniform rate of seed moisture decrease during seed development. These rates were 25 g kg^{-1} for 'Alta' tall fescue (Klein and Harmond, 1971) and 18 to 20 g kg^{-1} d^{-1} for perennial ryegrass (Hill and Watkin, 1975). The present study indicates, however, that more precise forecasting would be achieved by considering a two-phase drying curve with different drying rates in each phase.

Harvesting Losses

Natural Shedding. Natural seed shedding started late and at low seed moisture contents during Chesapeake and Emperor seed maturation (Fig. 2). Seed shedding was first observed at moisture contents lower than 170 g kg^{-1} in Chesapeake during 1991. During this year, seed shedding started earlier during seed development in Emperor and at a moisture content around 360 g kg^{-1}. Seed moisture was around 220 g kg^{-1} when seed shedding started in both cultivars during 1992.

The relatively earlier shedding in Emperor during 1991 can be attributed to the occurrence of strong winds on 19 and 20 June when wind speed was 70% higher than the average for the remaining of the seed maturation period. Lodging protected the Chesapeake plants from the wind and probably reduced and delayed losses by shedding until late in the seed development period. During 1992, when lodging was not important and seed maturation proceeded without weather disturbances, seed shedding started at about the same moisture content in both cultivars. In this year, the smaller amounts of seed shedding observed in Emperor were proportional to the lower yields obtained.

Factors such as species, varieties, lodging, wind, rain or hail can affect seed shedding (Jensen, 1976; Andersen and Andersen, 1980). With grasses like meadow fescue (Festuca pratensis Huds.), Jensen (1976) found seed shedding starting at moisture contents higher than those observed for Chesapeake and Emperor tall fescue. Physiological seed maturity occurs at moisture contents varying from 400 to 480 g kg^{-1} for these two cultivars (Chapter 4) and seed shedding occurred later than this. Elgersma et al. (1988) found that breaking of the abscission layer in perennial ryegrass occurred 5 wk after anthesis. The seeds, however, remained connected to the rachilla by a central cambium and the vascular bundles and a mechanical force was necessary to cause seed shedding. Although signs of seed shedding from inflorescences are indicative of the optimum harvesting time of some cool season grasses (Griffiths et al., 1976), this was not the case for Chesapeake and Emperor tall fescue. Without mechanical disturbance, natural seed shedding started too late during the seed maturation period to be a useful indicator of optimum harvesting time in windrow-harvested tall fescue.

Total Seed Losses. The total amount of seed lost on the ground after harvesting operations was inversely related to seed moisture at harvest during both years (Fig. 3). Total seed losses were smaller in 1992 for all cultivars. When windrowed around 400 g kg^{-1}, losses were 18, 34, and 25 % of the yield during 1991 for Chesapeake, Bonanza and Emperor, respectively, and 10, 13 and 14 % during 1992. Total seed losses increased at a rate of 35, 89 and 80 kg ha^{-1} for each 100 g kg^{-1} drop in the seed moisture content for Chesapeake, Bonanza, and Emperor, respectively, during 1991 with harvests between 550 and 200 g kg^{-1}. During 1992 those rates were 20, 15 and 5 kg ha^{-1}, respectively.

The air blowing through the combine screens was kept to a minimum in order to avoid seed losses and inspection of the straw revealed that very few seeds remained attached to the inflorescences after threshing. Therefore, seed shedding from the windrows and seed shattering during windrowing and combining were the main causes of seed loss in the plots. Lodging might explain the relatively smaller amount and rate of seed loss measured in Chesapeake during 1991. In this cultivar, the lodged inflorescences were not touched by the windrower reel and, since the plants were laying on the ground, shaking caused by the cutter bar was reduced. Lodging of Bonanza and Emperor was not severe enough to place the seed heads out of the reach of the reel or to reduce shaking caused by the cutter bar during windrowing.

The percentage of losses observed in the present study are smaller than the 38 % losses reported for Alta tall fescue by Klein et al. (1961). It is probable also that figures for losses measured in this study underestimated the losses occurring with farm-size machinery. The operating speed used by growers is around 6 - 8 km h^{-1} for windrowing and 5 km h^{-1} for combining. In contrast, operating speeds for harvesting the plots were 0.8 km h^{-1} for windrowing and 2 km h^{-1} for combining. Farm windrowers normally have an auger to place the cut material in windrows and most of the farm combines use drapers with wire fingers to lift the windrow from the ground and deposit it on the combine platform. The plot windrower used a draper system which tends to cause smaller seed losses during windrowing. Also, compared with the traditional pick-up with wire fingers, the pick-up attachment with rubber fingers on the plot combine caused smaller agitation of the windrows during combining.

Although Williams (1972) showed that pre-harvest losses reduced yield in tetraploid ryegrass, natural seed shedding in Chesapeake and Emperor occurred too late in the seed maturation period to be of concern. Occurrence of strong winds during seed development might, however, cause earlier seed shedding and reduce yield. Losses during harvesting operations reduce yields and supply the soil seed bank with seeds from which a generation of volunteer plants will infest the area. The amount of total losses observed in this study indicates that development of more efficient harvest machinery can be an alternative way to reduce losses and increase yield in turf-type tall fescue.

Yield

The seed moisture content indicative of maximum seed yield varied between cultivars and between years for the same cultivar (Fig. 4). For Chesapeake, the optimum seed moisture contents were 380, 340, and 310 g kg^{-1} respectively, during 1990, 1991 and 1992. For Bonanza, the optimum moisture varied from 410 in 1990 to 350 g kg^{-1} in 1992. For Emperor, optimum seed moisture was 360 g kg^{-1} in 1992. Lodging of plants increased the variability of the yield data, preventing a quadratic association between seed moisture content and yield to be expressed in one year for Bonanza and in two years for Emperor, and prevented comparison between the cultivars within those years (Fig. 4). The number of GDD at which maximum yields were achieved was also variable between years and cultivars (Fig. 5). A quadratic association between yield and GDD was detected in 1991 and 1992 for Chesapeake, 1990 and 1992 for Bonanza, and 1992 for Emperor. Maximum yields in Chesapeake were obtained at 360 and 354 GDD during 1990 and 1991. For Bonanza, 308 GDD in 1990 and 345 in 1992 were needed for maximum yield. For Emperor, maximum yield occurred when 306 GDD were accumulated in 1992 (Fig. 5).

Maximum yields in Chesapeake probably occurred at lower moisture contents because lodging reduced seed losses (Fig. 3 and 4). These results also corroborate Andersen and Andersen's (1980), statement that windrowing can be delayed to lower moisture contents when the seed crops lodges. The year-to-year variation and the relative flatness of the curves associating yield and seed moisture content support the approach used by Andersen and Andersen (1980) of recommending ranges of moisture contents for windrowing a number of species. Hill and Watkin (1975) and Arnold and Lake (1965) also indicated that maximum yield can be achieved with harvesting over a range of moisture contents because of completion of drying in the windrow. Further supporting the indication of a range of moisture contents for maximum yields, Evans (1959) suggested that in years without a well defined peak anthesis, a corresponding seed maturation plateau might occur on which maximum yield can be achieved.

The recommended harvest indexes for other cultivars of tall fescue (Klein and Harmond, 1971; Hare et al., 1990) are above the range of moisture contents found in this study for the three cultivars of turf-type tall fescue. Unfortunately, those authors did not present the year-to-year variation or the amount of total losses encountered, and speculation about possible causes for the differences between the studies is not possible.

The use of GDD as an alternative to days after anthesis as an indicator of harvest timing was suggested by Andersen and Andersen (1980). Although the estimated GDD for maximum yields was constant for 1990 and 1991 in Chesapeake, it was quite variable for Bonanza between 1990 and 1992 (Fig. 5). This indicates that GDD also has year-to-year variation and might not be an improvement as an indicator of optimum harvest timing.

Because of the small plot width (three rows harvested), whether plants lodged in or out of the plots had a relatively high influence on the yield and increased variability of the results. It is likely that the use of wider plots would reduce the relative influence of plants lodging on the sides of the harvested area and yield variability would be reduced.

Seed Weight and Germination

For all cultivars, seed weight tended to increase with harvests at successively lower moisture contents until a maximum weight was achieved at moisture contents below 450 g kg^{-1} (Table 4). A similar tendency was observed for a number of cool season grasses (Grabe, 1956; Hill and Watkin, 1975; Williams, 1972). Seed moisture content at physiological maturity varies with species. For example, maximum seed weight was achieved at 330 g kg^{-1} moisture content for three cultivars of red fescue (Hebblethwaite and Ahmed, 1978). Pegler (1976), studying harvest timing in S 170 tall fescue, related seed maturation to number of days after anthesis and to endosperm consistency. With hand harvesting, seed weight tended to level off approximately 30 d after peak anthesis or when endosperm consistency was at the cheesy or hard stage. For Chesapeake, Bonanza and Emperor, as an average, seed weight tended to level off from 20 to 28 d after peak anthesis.

Germination increased from the first harvest and tended to level after maximum values were achieved, usually during the third or fourth harvest (Table 4). During the three years for Chesapeake and during 1990 and 1991 for Bonanza, germination values above 95 % were obtained with harvests at moisture contents below 470 g kg^{-1}. For Emperor, 95 % germination was achieved at a seed moisture content of 440 g kg^{-1} during 1990 and 1991. Seed germination above 95 % was delayed until harvests at lower moisture contents in Bonanza and Emperor during the drier 1992 season. For the medium-maturity Bonanza, seed germination was above 95% with harvests at moistures below 400 g kg^{-1}. Apparently, those drier conditions were more detrimental to seed germination in the late-maturing Emperor. With this cultivar, germination of 95 % was achieved only with the last harvest at a moisture content of 210 g kg^{-1}.

Although seeds of several grass species are able to germinate 1 to 2 wk after anthesis (Pegler, 1976; Roberts, 1969 and 1971), maximum seed vigor occurs only when seeds achieve maximum dry weight (Grabe, 1956), and this characteristic needs to be considered in defining the optimum harvesting time. For the three cultivars, maximum seed weight and germination above 95 % are likely to occur with harvests at moisture contents lower than 450 g kg^{-1}. During dry years this tendency might change and, mainly for late cultivars, high seed germination might only be achieved with harvests at lower moisture contents.

Conclusions

Maximum yields were achieved by windrowing at moisture contents in the range of 350 to 410 g kg^{-1}. In this range, maximum dry seed weight and germination percentage were achieved and natural seed shedding was minimal. It is unrealistic to recommend a narrower range or a specific moisture content to indicate optimum harvest time in tall fescue because of uneven maturity caused by an extended flowering period, lodging of plants, and yearly climate conditions. These factors and the considerable plant-to-plant variation within cultivars made it impossible to discern cultivar-specific requirements for optimum harvest timing in relation to moisture content.

Loss of seed moisture during tall fescue seed maturation occurs in two phases. During the first phase, moisture decreased about 11 g $kg^{-1}d^{-1}$. At about 500 g kg^{-1}, moisture loss accelerated, decreasing about 35 g $kg^{-1}d^{-1}$. It is necessary to understand this two-phase moisture loss pattern to realistically predict when the target seed moisture content for harvest will occur. The 350 to 410 g kg^{-1} moisture range represents about a 2-d window for optimum harvest timing.

Table 5.1. Precipitation and temperature during the reproductive development of Chesapeake, Bonanza, and Emperor tall fescue.

Month	Precipitation			Average Temperature		
	1990	1991	1992	1990	1991	1992
	mm			°C		
January	241 (+50)†	68 (-124)	116 (+59)	5.7 (+1.3)	7.8 (+0.1)	6.3 (+1.4)
February	147 (+24)	82 (-42)	116 (+13)	4.6 (-1.2)	9.1 (+3.0)	8.6 (+2.6)
March	56 (-61)	149 (+31)	27 (-90)	8.8 (+1.5)	7.1 (-0.2)	10.5 (+2.7)
April	60 (-2)	88 (+26)	104 (+39)	10.3 (+2.2)	9.5 (-0.7)	12.2 (+3.0)
May	36 (-12)	99 (+51)	0 (-50)	12.5 (-1.0)	11.4 (-1.3)	15.9 (+3.2)
June	39 (+8)	39 (+8)	30 (-1)	16.7 (+0.4)	14.2 (-1.7)	18.7 (+2.5)
July	11 (+4)	10 (+2)	30 (+17)	19.5 (+1.8)	19.6 (+0.9)	20.3 (+1.5)

† Numbers in parentheses refer to the departure from normal for the previous 10 years.

Table 5.2. Daily GDD accumulation after mid-anthesis and rates of seed moisture decrease during the two phases of moisture loss in tall fescue cultivars.

	First drying phase (P1)			Second drying phase (P2)		
		Rate of moisture loss			Rate of moisture loss	
Year	Daily GDD†	per GDD	per day††	Daily GDD	per GDD	per day
		$g\ kg^{-1}$			$g\ kg^{-1}$	
			Chesapeake			
1990	14.24	0.73 a§	10.4	13.68	2.5 b	34.2
1991	15.37	0.77 a	11.8	15.70	3.1 a	48.9
1992	14.56	0.96 a	13.0	14.53	2.4 b	35.0
			Bonanza			
1990	14.95	0.83 a#	12.0	14.69	2.9 a	42.2
1991	15.88	0.73 a	12.0	15.54	3.4 a	52.2
1992	12.86	0.58 a	7.4	18.65	2.3 a	42.5
			Emperor			
1990	14.00	0.80 a	11.2	18.33	2.7 a	49.0
1991	15.47	0.72 a	11.0	16.16	2.1 a	34.0
1992	12.67	0.47 a	5.9	18.63	2.0 a	38.0

† Calculated from (GDD accumulated in the period)*(number of days in the period)$^{-1}$.

†† Calculated from ($g\ kg^{-1}\ GDD^{-1}$)*(Daily average GDD accumulated).

§ Rates followed by different letters differ at F test ($p \leq 0.05$).

Non-uniform variance prevented the comparison 1990x1991 for the first drying phase in Bonanza. Letters refer to the remaining comparisons.

Table 5.3. Seed moisture content, GDD and days after mid-anthesis at the beginning of phase 2 of moisture loss.

Year	Seed moisture†	GDD‡	Days§
	g kg^{-1}		d
		Chesapeake	
1990	510	288	20
1991	500	297	19
1992	460	299	21
		Bonanza	
1990	460	313	21
1991	510	361	23
1992	510	308	24
		Emperor	
1990	490	282	20
1991	510	306	20
1992	510	221	17

† Estimated from the spiline models fitting the moisture loss for each cultivar each year.

‡ GDD value for the joint point of the spiline model fitting the moisture loss with the smallest mean square error.

§ Days after peak anthesis.

Table 5.4. Seed weight and germination of tall fescue cultivars windrowed at different seed moisture contents.

1990			1991			1992		
Windrowing moisture	Seed weight	Germi-nation	Windrowing moisture	Seed weight	Germi-nation	Windrowing moisture	Seed weight	Germi-nation
$g\ kg^{-1}$	mg	%	$g\ kg^{-1}$	mg	%	$g\ kg^{-1}$	mg	%
				Chesapeake				
560	2.00 d†	94.7 d	570	1.90 c	91.9 b	540	1.79 b	87.8 d
480	2.32 c	96.5 cd	490	2.24 b	94.7 ab	490	1.87 b	95.1 c
440	2.45 b	96.9 bc	400	2.31 ab	96.0 a	430	2.21 a	97.1 bc
380	2.46 b	97.7 bc	330	2.36 a	96.2 a	380	2.22 a	97.9 ab
270	2.53 ab	97.8 ab	230	2.37 a	96.9 a	210	2.25 a	98.1 ab
230	2.55 a	98.5 a	170	2.42 a	97.2 a	100	2.27 a	99.1 a
				Bonanza				
560	1.96 d	92.4 b	560	1.79 b	83.4 b	580	1.65 c	83.9 d
510	2.14 c	91.8 b	470	2.14 a	94.6 a	520	1.89 c	90.1 c
480	2.44 b	65.6 a	400	2.17 a	95.4 a	430	2.16 b	92.5 bc
410	2.45 ab	96.1 a	300	2.19 a	96.1 a	400	2.22 b	93.9 ab
360	2.54 a	96.2 a	220	2.26 a	96.5 a	300	2.32 a	94.0 ab
280	2.54 a	97.3 a	160	2.28 a	96.6 a	170	2.32 a	95.6 a
				Emperor				
550	2.01 d	91.5 a	550	1.90 c	84.7 d	590	1.63 d	72.1 c
500	2.11 cd	93.0 a	440	2.24 b	95.1 c	510	1.88 c	73.0 c
440	2.15 bc	94.5 a	380	2.31 ab	95.8 bc	470	2.07 b	78.1 c
390	2.18 abc	94.6 a	310	2.36 a	96.0 bc	360	2.17 a	85.5 b
350	2.25 ab	94.6 a	240	2.37 a	97.1 ab	270	2.19 a	86.1 b
300	2.28 a	94.6 a	190	2.42 a	97.9 a	210	2.20 a	95.3 a

† Dry seed weight and germination percentage followed by a different letter are significantly different according to the LSD test at $p \leq 0.05$.

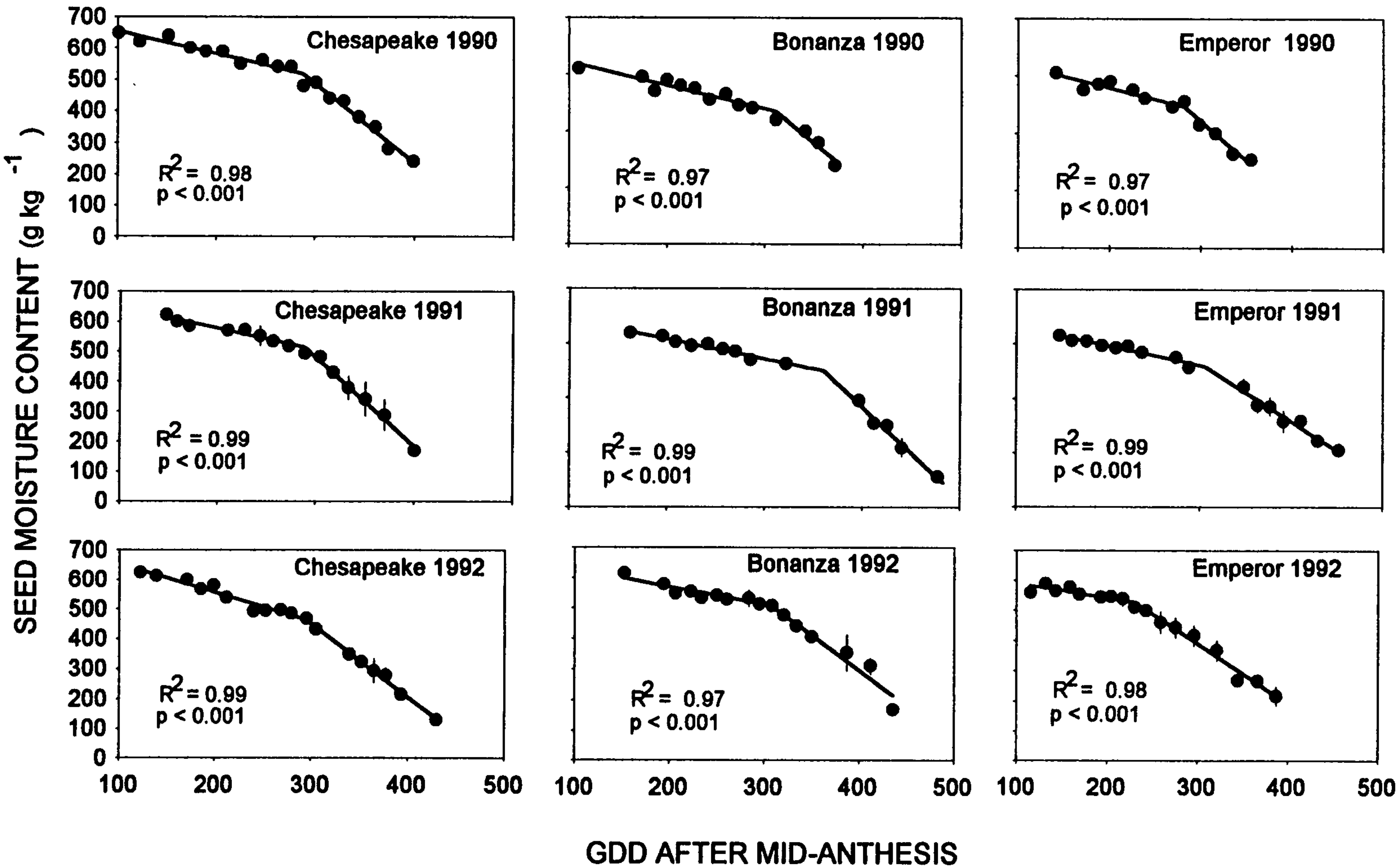

Fig. 5.1. Relationship between GDD after mid-anthesis and moisture loss during seed development in tall fescue. Vertical lines represent the mean standard error (n=4). For some data points the standard error was smaller than the symbol. Mean standard error was not calculated in 1990.

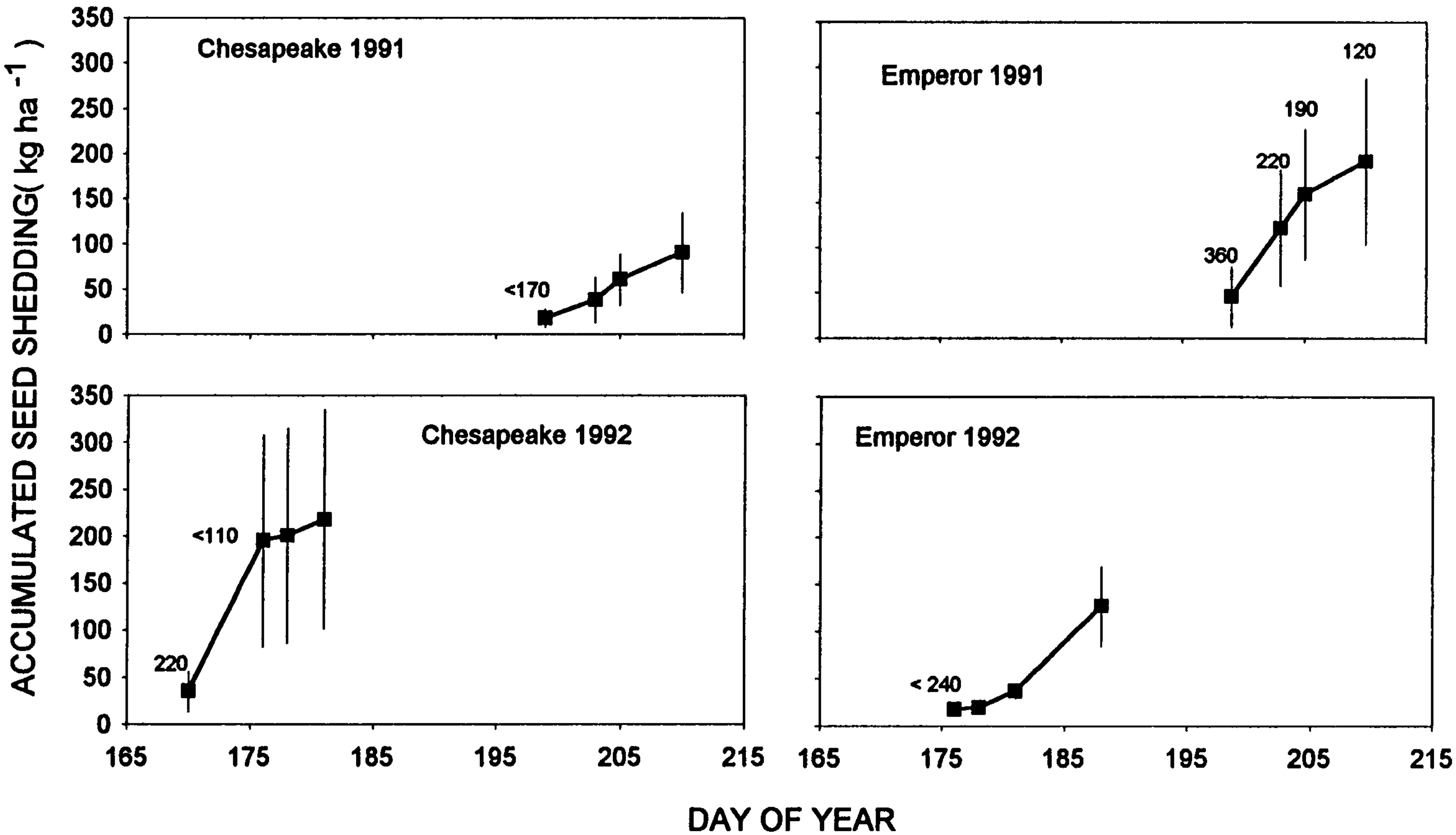

Fig. 5.2. Natural seed shedding in tall fescue. Numbers inside the graphs are seed moisture content in g k $^{-1}$ at that sampling date. Vertical lines represent the mean standard error (n=16). For some sampling dates the mean standard error was smaller than the symbol.

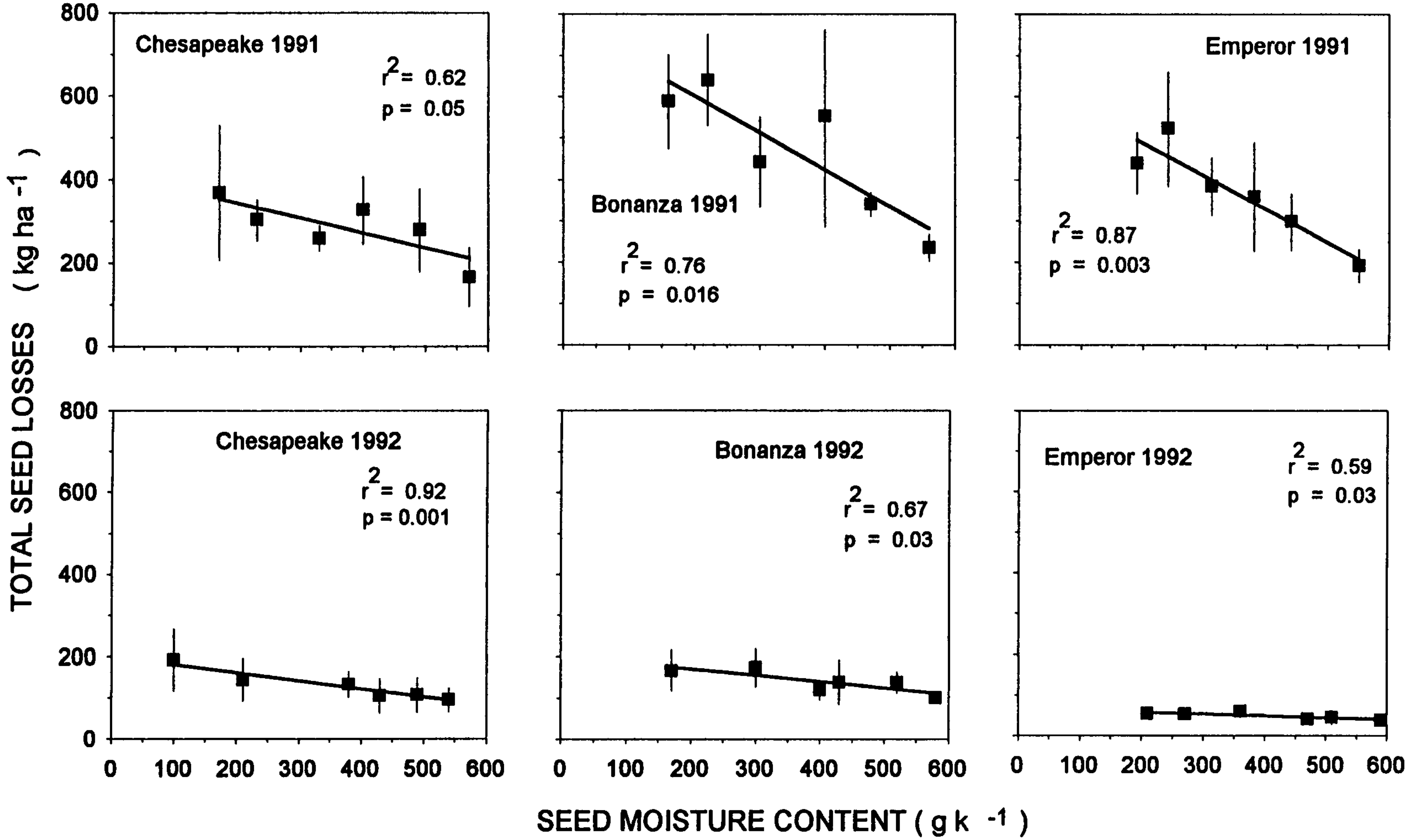

Fig. 5.3. Effect of seed moisture content at windrowing on total harvest losses in tall fescue cultivars. Vertical line represent the mean standard error (n=12). For some moisture contents the mean standard error was smaller than the symbol.

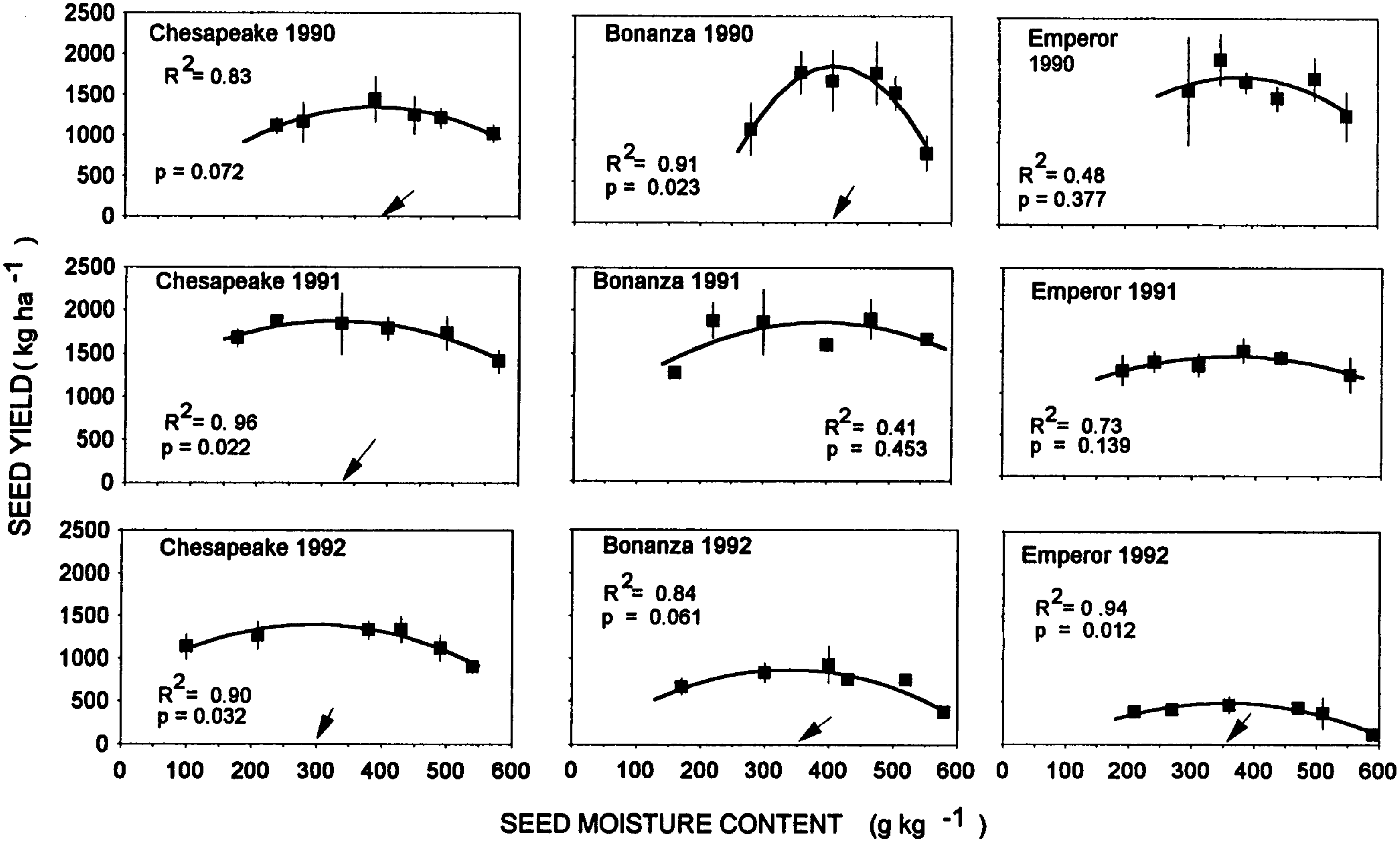

Fig. 5.4. Effect of seed moisture content at windrowing on seed yield in tall fescue cultivars. Arrows indicate moisture content for maximum seed yield. Vertical lines represent the mean standard error for each harvest (n=4). For some harvests the mean standard error was smaller than the symbol.

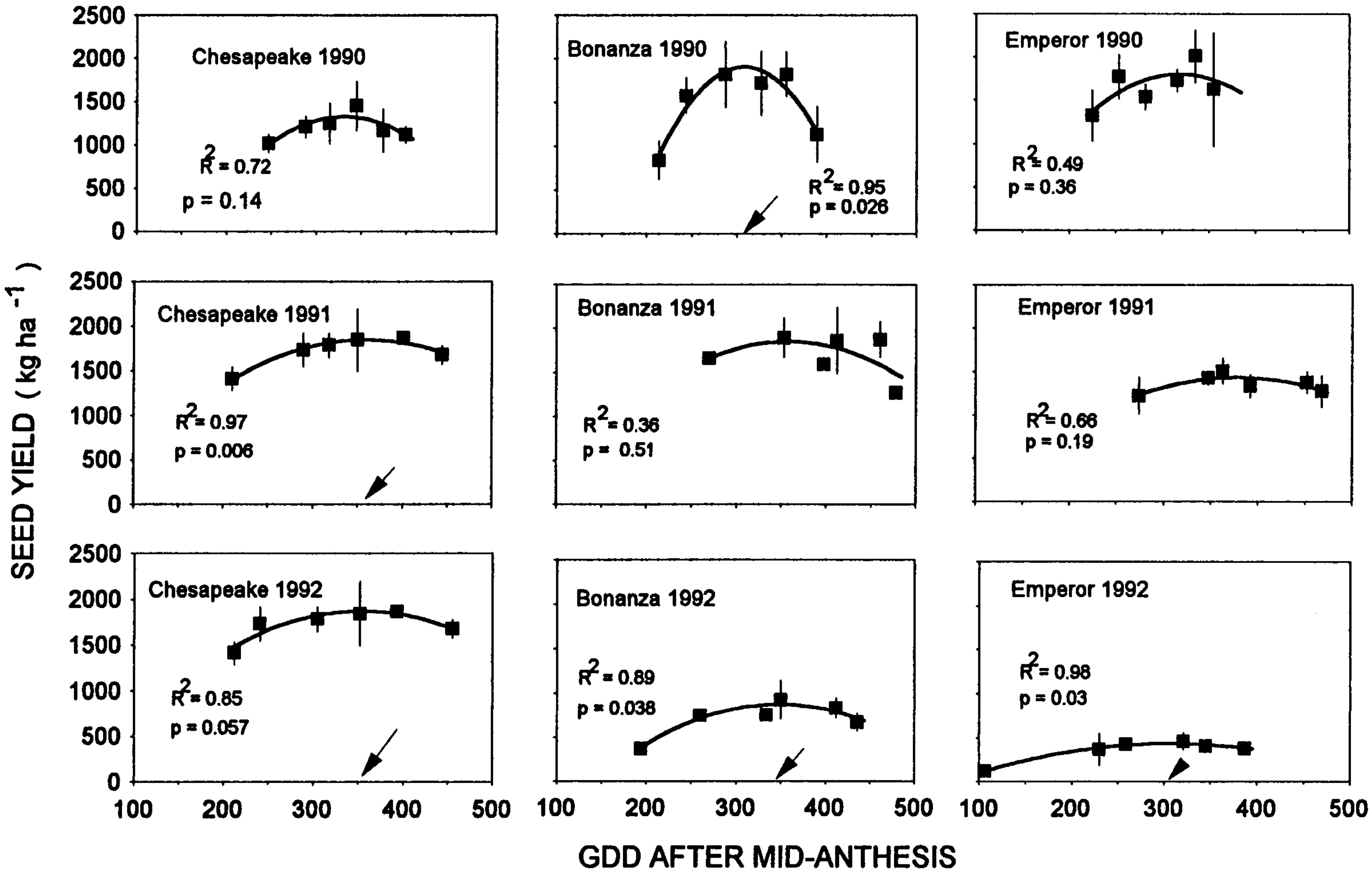

Fig 5.5. Effect of GDD after anthesis at windrowing on seed yield in tall fescue cultivars. Arrows indicate GDD for maximum seed yield. Vertical lines represent the mean standard error for each harvest (n=4). For some harvests the mean standard error was smaller than the symbol.

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