AN ABSTRACT OF THE THESIS OF

Carlos Alberto García-Díaz for the degree of Doctor of Philosophy in Crop Science presented on June 13, 1997. Title: Water Management Effects on Birdsfoot Trefoil Seed Production.

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Jeffrey J. Steiner

There is no information available on water management of birdsfoot trefoil grown for seed. Information is also not available describing how to minimize seed losses due to shattering in order to obtain consistently high birdsfoot trefoil seed yields. The objectives of this research are to: (i) quantify crop water use, effects of soil-water availability and optimal water management conditions for birdsfoot trefoil grown for seed, (ii) determine the effects of irrigation timing and amount on flower production, seed yield, and yield components, and (iii) quantify the effects of soil-water availability on seed shattering and determine optimal harvest time to reduce seed yield losses due to shattering. Five supplemental irrigations treatments and a non-irrigated control were applied in 1994 and 1995; in 1996, only treatments low stress and non irrigated control were investigated, near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll).

Increasing amounts of applied water increased seasonal ET_c with low stressed plants having the greatest ET_c and non-irrigated control plants the least. The fraction of available soil-water used was primarily dependent upon the irrigation depletion percentage and secondarily dependent upon irrigation replacement amount. Soil-water conditions favorable for vegetative development and seed yield water use efficiency are opposite. Birdsfoot trefoil grown for seed requires minimal or no supplemental irrigation. For non-irrigated conditions, the crop water requirement ranges from 240 to 255 mm.

In the first year of production, plants under low-stress conditions sustained flowering longer than with limited or no irrigation applications. Flowering was not affected by irrigation in subsequent years of production. Total above-ground phytomass production was correlated with the amount of applied irrigation water ($r = 0.92$). Umbel density and number of seeds per pod are the primary determinants of total seed yield ($r = 0.77$ and 0.92, respectively).

Manipulation of the reproductive development pattern by different water application times and amounts does not affect peak seed shattering events. Crop-water stress status affects the percentage of total shattered seeds shattered at harvest time ($r = -0.76$). Increasing amounts of applied water increase the percentage of potential shatter losses that will shatter by harvest time ($r = 0.65$). Seed shatter losses fluctuate during the reproductive development period but are not influenced by the water application treatments. Climatic variables as measured in this experiment cannot be used to predict the time of peak seed shatter events. A total of 109 heat units are needed from the time from initial pod dehiscence until rapid shattering occurs.

WATER MANAGEMENT EFFECTS ON BIRDSFOOT TREFOIL SEED PRODUCTION

by

Carlos Alberto García-Díaz

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Carlos Alberto García-Díaz

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DEDICATION

This thesis is especially dedicated to the lovely memory of my parents:

J. Guadalupe García L.

and

Ma. Mercedes Díaz de G.

WATER MANAGEMENT EFFECTS ON BIRDSFOOT TREFOIL SEED PRODUCTION

CHAPTER 1

GENERAL INTRODUCTION

Birdsfoot trefoil (*Lotus corniculatus* L.) is a perennial, non-bloating forage legume used for pasture, hay, and silage in the midwestern and northeastern USA and eastern Canada. It is adapted to a wide range of soil conditions and environments where other popular legumes may not perform well.

Most birdsfoot trefoil seed is grown in the northcentral and northeastern USA (AOSCA, 1994). Annual certified seed production is estimated to be about 83 t from 830 ha. Seed yields range from 50 to 560 kg ha^{-1} (Seaney and Henson, 1970; McGraw and Beuselinck, 1983; White et al., 1987; Li and Hill, 1989;) with 50 to 170 kg ha^{-1} considered as average (Seaney and Henson, 1970; McGraw and Beuselinck, 1983; Winch et al., 1985) and 400 kg ha^{-1} as excellent (McGraw and Beuselinck, 1983). Research has been carried out on birdsfoot trefoil seed production and some of the most important limiting factors have been identified (Fairey, 1994). Seed shattering has been considered a major problem in birdsfoot trefoil seed production (Seaney and Henson, 1970; Li and Hill; 1989). Although the wide range in seed yield is in part due to shattering, soil-water availability may also be a factor that constrains birdsfoot trefoil seed yields. There is no information available on water management of birdsfoot trefoil grown for seed. Information is also not available describing how to minimize seed losses due to shattering in order to obtain reliable, consistent, and high birdsfoot trefoil seed yields.

The criteria considered to be the most important for highest seed yields are: (i) a rapid, and compact period of flower emergence and pod development (fast flower differentiation), (ii) weather conditions that benefit seed development, and (iii) proper harvest timing when the highest pod maturity percentage of the plant population is reached to minimize seed losses caused by shattering.

Water management practices for maximal seed production of forage legume seed crops are distinct from those for hay or pasture crops (Hutmacher et al., 1991; Steiner et al., 1992). In forage legume seed crops, different responses to both high and low soil-water availability amounts are found. In most crops, an optimal amount of water is needed to promote flower development, pollination, seed growth and maturation. Water management effects on forage legume seed production vary among species. Species have distinct responses for water stress adjustment and there is not a general water management strategy for all forage legume seed crops. Alfalfa and white clover seed yields can be optimized by limiting the plant vegetative growth by controlled water stress (Clifford, 1985; 1986; Steiner et al., 1992, Oliva et al., 1994c). Red clover, however, responds optimally when there is no or low water stress during the reproductive phase of growth (Oliva et al., 1994b). Optimal irrigation management also can differ between the years when the crop is first established to that of successive years of seed production (Oliva et al., 1994a; 1994c) and by the quantity of stored water into the soil profile during the winter (Steiner et al., 1992).

Birdsfoot trefoil is adapted to a wide range of soil conditions and environments. However, there is no information available about the crop water requirements for birdsfoot trefoil grown for seed. Some literature is available for birdsfoot trefoil forage crop water use. When water is applied to maintain 50 - 75% soil-water depletion (stress) and at 35% depletion (low-stress), stem water potentials range from -1.0 to -3.8 MPa and -0.1 to -1.4 MPa, respectively (Peterson et al., 1992). Birdsfoot trefoil herbage production in Montana does not respond to supplementary irrigation. Herbage yields average 6.3 to 7.2 Mg ha^{-1} and the plants show no evidence of wilting on non-irrigated treatment, even when upper soil depths were at or near the wilting point (Cooper, 1961).

The most important birdsfoot trefoil seed yield component is the number of umbels or inflorescences per unit area (Albretchsen et al., 1966; Bresciani and Frakes, 1973; Pankiw et al., 1977; McGraw et al., 1986a; Stephenson, 1984; Li and Hill, 1988; 1989). Management practices that reduce the number of umbels per unit of area will ultimately decrease seed yield. When the number of umbels are not limited, yield components such a number of florets per umbel, number of seeds per pod, number of pods per umbel, and seed weight may influence seed yield.

Seed losses can result from seed shatter after pod maturation at harvest time. A delay in the seed harvest to allow the latest developing umbels to mature can result in a decrease in the seed yield of approximately 50 (Winch and MacDonald, 1961) to 67% if harvest is delayed nine days after the time of maximum percentage of pod maturation (Anderson, 1955).

Seed shatter occurs when the relative humidity is below 40% (Anderson, 1955). However, when temperatures are high and relative humidity high, the rate of shattering is less than at high temperatures in drier environments (Metcalfe et al., 1957; McGraw and Beuselinck, 1983). A high rate of shattering is caused by a rapid loss of moisture from the pods. However, shattering does not rapidly progress when drying proceeds slowly (Buckovic, 1952).

Because of the indeterminate flowering nature of birdsfoot trefoil, harvest timing is a critical factor that influences final seed yield (Seaney and Henson, 1970; Li and Hill; 1989). The optimal time for harvest has been reported to be predicted by the appearance time of the pods and pod color (Anderson, 1955; Winch and MacDonald, 1961; Hare and Lucas, 1984; Pieroni and Laverack, 1994) and the rate of development of reproductive parts (Li and Hill, 1989). High yields of good quality seeds are obtained if birdsfoot trefoil is harvested when pods are light green to light brown (Anderson, 1955; Winch and MacDonald; 1961; Pieroni and Laverack, 1994). This corresponds to a proportion of 60 to 85% of mature to total pods (Winch and MacDonald, 1961). In New Zealand, harvest timing is recommended to be 35 days after maximal number of inflorescence are achieved, since this is the time required for blooming flowers to develop into mature pods. Pod color is used as a secondary guideline (Li and Hill, 1989).

The objectives of this research are to: (i) quantify crop-water use, effects of soil-water availability, and the optimal water management conditions for birdsfoot trefoil grown for seed, (ii) determine the effects of irrigation timing and amount on flower production, seed yield, and yield components, and (iii) quantify the effects of soil-water availability on seed shattering and determine optimal harvest time to reduce seed yield losses due to shattering. The results of these studies are presented in three chapters. Chapter 3 describes the study to accomplish objective (i), Chapter 4 comprises the study to achieve the objective (ii), and Chapter 5 encompasses the study to achieve the objective (iii).

CHAPTER 2

LITERATURE REVIEW

Birdsfoot trefoil is a perennial, non-bloating forage legume, with a long, vigorous taproot, and numerous lateral branches that form a dense fibrous root system in the upper 30-60 cm of soil. Birdsfoot trefoil roots do not penetrate the soil as deeply as alfalfa, but surpass those of red clover in depth and distribution (MacDonald, 1944). Birdsfoot trefoil growth is from upper axillary buds on the upper stem bases (Smith, 1962; Nelson and Smith, 1968). The transition from a vegetative to a reproductive apex starts by a broading and lobing of the stem tip. Each lobe is a flower primordium subtended by a small bract (Hansen, 1953). Stems arise from a single crown and can reach lengths up to 90 cm (Grant and Marten, 1985).

Birdsfoot trefoil flowering habit is indeterminate, so flowering is extended over a long period of time (McGraw and Beuselinck, 1983; Li and Hill, 1988). Flowering occurs from continuous shoot succession with continued shoot replacement as older shoots die. New shoots become fertile under appropriate conditions for flower induction (Li and Hill, 1988). However, even with a prolonged flowering period, more than 70% of the inflorescences are formed during a relatively short 25-day period (Li and Hill, 1988).

Birdsfoot trefoil is a long-day plant that requires 16 h of light for full flowering with a critical photoperiod of 14 h (Joffe, 1958; McKee, 1963). Shorter daylengths constrain flower development and results in plants having a more prostrate growth form. At latitudes higher than 30° N, photoperiodic requirements are met in spring and result in fast and abundant flowering (McKee, 1963). Cooler spring temperatures provide a more favorable environment to initiate the onset of flowering than warmer temperatures (Smith, 1970).

The inflorescence is an umbel consisting of four to eight florets attached by short pedicels to a long peduncle (Seaney and Henson, 1970). The number of ovules per ovary vary from 20 to 72, of which up to 45% develop into mature seeds (Giles, 1949; Hansen, 1953; Bubar, 1958; Wojciechowska, 1963).

An average of three to six long cylindrical pods are borne at right angles to the tip of the peduncle which gives the appearance of a bird's foot. Each pod contains an average of 19 seeds, ranging from two to 35 seeds (Hansen, 1953). The seeds are small with hard seed coats when mature (Seaney and Henson, 1970). The low seed set percentage in birdsfoot trefoil can be due to the differential maturation of ovules within an ovary and to the depletion of the stigmatic fluid supply (Bubar, 1958).

At maturity, pods split along sutures and twist spirally to discharge the seeds (Seaney and Henson, 1970). Shattering is the result of the tension that is thought to overcome the cohesion between the exocarp and mesocarp pod layers. This tension is likely affected by a gradient of pod moisture content (Buckovic, 1952; Fahn and Zohary, 1955).

Birdsfoot trefoil is a largely self-incompatible species with a low percentage of plants exhibiting self-compatibility (Silow, 1931; MacDonald, 1944; Bubar, 1958; Wojciechowska, 1963). Seed set mainly results from insect cross-pollination (Seaney and Henson, 1970; Grant and Marten, 1985). Autogamy is also found in birdsfoot trefoil (Steiner, 1993; Steiner and Poklemba, 1994).

Several factors restrict the seed yield potential of birdsfoot trefoil. Low assimilate partioniting to seeds (McGraw and Beuselinck, 1983), indeterminate flowering that results in uneven pod maturity, and rapid seed shattering allow only a small proportion of the potential seed yield to be realized at harvest (Seaney and Henson, 1970; Grant and Marten, 1985). Under optimal conditions, potential seed yields can reach 1100 to 1200 kg ha^{-1} (Seaney and Henson, 1970; Grant and Marten, 1985). Harvest timing is a critical factor affecting the resulting final seed yield recovery (Li and Hill, 1989). The indeterminate flowering habit makes it difficult to decide when to harvest birdsfoot trefoil grown for seed (Anderson, 1955; Metcalfe et al., 1957; Winch and MacDonald, 1961; Seaney and Henson, 1970; McGraw and Beuselinck, 1983).

Effects of Soil-Water Availability on Birdsfoot Trefoil Seed Yield

Most research regarding birdsfoot trefoil seed production comes from studies done in the northcentral USA and southcentral Canada. There are no reports for water management on birdsfoot trefoil seed production.

Most seed crop water management research comes from California (carrots, Steiner et al., 1990; cowpea, Ziska and Hall, 1983a; 1983b, Ziska et al., 1985; lima bean, Ziska and Hall, 1983b; Ziska et al., 1985). Water management research for seed production of forage legume seed crops has been done with alfalfa (Taylor et al., 1959; Yamada et al., 1973; Hageman et al., 1975; Beukes and Barnard, 1985; Steiner et al., 1992), red clover (Oliva et al., 1994a, 1994b) and white clover (Zaleski, 1966; Clifford, 1985; 1986; Danyack-Deschamps and Wery, 1988; Bullita et al., 1988; Oliva et al., 1994c, 1994d).

The effect of water stress on plant growth and seed yield is different among seed crops, depending on the time when the stress occurs. In an indeterminate flowering species such as carrot (*Daucus carota* L.), optimal seed yield was achieved by a gradually accumulating water stress using deficit irrigations. Increasing water deficit improved seed quality by limiting the development of later maturing inflorescences and reducing umbel competition for photosyntates and reserves (Steiner et al., 1990).

With cowpeas (*Vigna unguiculata* [L.] Walp.), withholding irrigation during the vegetative stage following pre-irrigation results in negligible effects on seed yield. Seed yield is reduced as plant water stress increases, mainly with 15-day irrigation interval (Ziska and Hall, 1983a) corresponding to a soil-water depletion of 60% (Ziska and Hall, 1983b). In another soil type with lower soil bulk density, vegetative stage stress did not affect cowpea or lima bean (*Phaseolus lunatus* L.) seed yield. Increasing soil-water depletion prior to irrigation up to 75% does not affect cowpea seed yield, but lima bean seed yield is reduced (Ziska et al., 1985).

Forage legume seed crops water management practices are different from those for forage production (Taylor et al., 1959; Hutmacher et al., 1991; Steiner et al., 1992). Maximal seed yield can be obtained by controlling supplemental water applications (Steiner et al., 1992). In alfalfa (*Medicago sativa* L.), low seed yields result when high water application amounts induce excessive vegetative plant growth (Taylor et al., 1959; Yamada et al., 1973; Hageman et al., 1975; Beukes and Barnard, 1985; Steiner et al., 1992) or when plants severely water-stressed restricts plant growth (Hageman et al., 1975; Steiner et al., 1992). Vegetative growth increases as water application amounts increase (Steiner et al., 1992). Optimal seed production results when soil-water is maintained wet from the time of initial regrowth in the spring until the beginning of the flowering period and then withholding water to increase the stress so that only the stored soil-water is used so that the soil-water matrix is -1.5 MPa at 1.8 m soil depth prior seed harvest (Taylor et al., 1959). The percentage of flowers that produce seed pods is reduced as water application increases, though the number of flowers produced increases (Cohen et al., 1972; Steiner et al., 1992). Seed yield is maximized when continued slow plant growth is achieved that promotes flower production and seed development while restricting excessive vegetative growth (Taylor et al., 1959; Yamada et al., 1973, Hageman et al., 1978, Beukes and Barnard, 1985; Steiner et al., 1992). Seed yields can also be maximized using a combination of lower pre-clipback irrigation and intermediate-level post-clickback water replacement during flowering and seed development (Steiner et al., 1992). Approximately 780-800 mm of seasonal water is used by replacing 70% of the 75 mm of ET_c utilized during the two subsequent seed crop years following the establishment year. When herbage production was evaluated for stressed and low-stressed alfalfa plants, the stem water potential ranged from -1.7 to -3.7 and -0.2 to -1.4 MPa, respectively (Peterson et al., 1992).

Water management for white clover seed production (*Trifolium repens* L.) is similar to that of alfalfa. With properly timed water applications that restrict vegetative development during the flowering period, floral density and seed yield are increased (Zaleski, 1966; Clifford, 1986; Bullita et al., 1988; Danyach-Deschamps and Wery, 1988; Oliva et al., 1994d). The duration of the flowering period is extended as crop water stress levels are decreased. Total above-ground phytomass production increases with decreasing average seasonal crop water stress index (CWSI) as measured by infrared thermometry. For a first year-seed crop, the average daily ET_c decreases as soil-water depletion increases. In a second year seed crop, plant water stress level did not affect seed yield. Seed bearing flower production is less than the first year due to a higher stolon density, affecting the balance between reproductive and vegetative development (Oliva et al., 1994d). Seed yield water-use efficiency is maximized with a single water application when the soil-water content has been depleted 68%. Under these conditions, the crop-water requirement was 310 mm (Oliva et al., 1994c).

For red clover (*Trifolium pratense* L.) seed production, optimal crop water management differs from that of alfalfa and white clover (Steiner et al., 1992; Oliva et al., 1994b). Both the flower bud growth and flower production periods are shortened by increasing levels of plant water stress (Oliva et al., 1994b). Total above-ground phytomass increases linearly as seasonal ET_c increases. Seed yield decreases as the level of plant water stress increases due to decreased floral fertility and flower density (Oliva et al., 1994b). Highest seed yield and water-use efficiency are achieved from a single irrigation that refills the 1.6 m active soil profile at peak flowering (Oliva et al., 1994a; 1994b). Under these conditions, the seed crop water requirement is 280 mm in the first year seed crop and 340 mm the following year (Oliva et al., 1994a). As a forage crop, red clover evaluated under water stressed and low water stressed conditions produced stem water potentials ranging from -1.7 to -3.7 and -0.2 to -1.4 MPa, respectively (Peterson et al., 1992).

Birdsfoot trefoil is adapted to a wide range of soil conditions and environments. No research has been done to determine the water management requirements for optimal birdsfoot trefoil seed production, but some literature is available for forage crop water use.

To evaluate herbage yield of birdsfoot trefoil in Minnesota, water was applied to maintain the extractable soil-water between 50 and 75% depletion (water stressed plants) and 85% of field capacity when 35% depletion of the soil-water availability occurred (low water stressed plants) (Peterson et al., 1992). Stem water potentials for stressed and low stress-plants ranged from -1.0 to -3.8 and -0.1 to -1.4 MPa, respectively. In two years (July 1987 and 1988), stem water potentials for the stressed and low-stress birdsfoot trefoil plants ranged from -1.6 to -3.6 and -0.1 to -0.4 MPa, respectively. Herbage yield of stressed plants averaged 21% less than low stressed plants.

Cooper (1961) in Montana concluded that birdsfoot trefoil herbage production did not respond to supplementary irrigation due to the presence of a shallow water table. Herbage yields averaged from 6.3 to 7.2 Mg ha^{-1} and the plants showed no evidence of wilting on the non-irrigated treatment, even when upper soil depths were at or near the wilting point. Soil-water content for non-irrigated plots to a soil depth of 1.8 m in June and August 1958 were at field capacity.

Birdsfoot trefoil has been shown to be a species well-adapted to withstand drought. Based on leaf extension rate, birdsfoot trefoil is the second top-ranked species for water stress resistance and recovery following stress (Davis et al., 1994). Drought resistance of birdsfoot trefoil has also been demonstrated under field grazing conditions. In Ohio, in a comparison of the mixtures of birdsfoot trefoil-Kentucky bluegrass and ladino clover-bluegrass for pasture, ladino clover was eliminated from the grazed stands by drought.

Birdsfoot trefoil persisted in the mixture when grazed with a rotational grazing system for the three years of the study (Davis and Bell, 1957).

Depth of penetration of the root system is a vital factor related to drought resistance (Whyte et al., 1953). In Australia, the success of birdsfoot trefoil in droughted habitats is due to a high root/shoot ratio and development of a strong deep taproot that reduces adult plant mortality (Foulds, 1978). Forage legume seed crops have different responses for water stress adjustment and birdsfoot trefoil grown for seed may have distinct response for soil-water availability due to its indeterminate nature and extensive root zone.

Effects of Soil-Water Availability on Seed Yield Components

The effects of soil-water availability on seed yield components are known for some forage legume crops. In white clover, controlling soil-water content is considered the easiest means to control seed yield on high fertility soils (Clifford, 1987). Irrigation is beneficial when applied at the beginning of flowering period. During flowering, irrigation increases vegetative growth with a detrimental effect on inflorescence production and seed yield (Zaleski, 1966; Clifford, 1985). The higher the soil-water content, the greater is the amount of above-ground phytomass. However, excessive growth can be controlled by limiting soil-water availability (Clifford,1985). Daynack-Deschmaps and Wery (1988) and Bullita et al. (1988) in Mediterranean environments reported that seed yield increased when water application amounts were reduced 20%. Constraining soil-water content reduces leaf size so more inflorescences (with lower floret numbers) are induced which consequently results in higher seed yields (Clifford, 1985). Both proper amount and timing of water application during the flowering period limits vegetative growth and increase reproductive development (Zaleski, 1966; Clifford, 1985; Clifford, 1986; Danyack-Deschamps and Wery, 1988; Bullita et al., 1988; Oliva et al., 1994d).

The reduction of floret number per inflorescence is caused by decreased soil-water availability, but is compensated by increased number of inflorescences per unit area (Clifford, 1986; Oliva et al., 1994d). In New Zealand, 50% replacement of available soil-water "near wilting" increased seed yield by increased inflorescence number, seed weight, number of seeds per inflorescence, and reduced ovule abortion compared to non-irrigated plants (Clifford, 1986).

In western Oregon, the seed yield components affected by irrigation treatments were inflorescence density and seed weight in the first-year seed crop. Only inflorescence density was affected in the second-year. Vegetative growth was vigorous in all irrigated treatments in the first-year crop and did not increase seed yield in a second year crop for any irrigated treatment (Oliva et al., 1994d). Because birdsfoot trefoil growth is indeterminate, seed yield depends on the rate of inflorescence production, length of flowering time, and the effective pollination period (Winch and MacDonald, 1961).

Little is known about the effects of soil-water availability on birdsfoot seed yield components. In Australia, by comparing the potential seed production of several forage legumes at different moisture levels, the number of florets per flowers of white clover and *M. lupulina* L. decreased when grown in droughted soil, but no difference was reported for birdsfoot trefoil (Foulds, 1978). Soil moisture level had no effect on the number of seeds per floret in white clover and *M. Lupulina* L., but birdsfoot trefoil had a slightly greater number in moist compared to droughted conditions (11 and 9 seeds, respectively) (Foulds, 1978). No differences were found in total seed production in birdsfoot trefoil and white clover in either of the two water regimes. Forage legume seed yield components are influenced by water management. Birdsfoot seed yield components may also be affected by soil-water-availability, the time of water stress, and the amount of water irrigation applied.

Factors affecting Seed Shattering and Harvest Timing

Seed shattering is a major problem in birdsfoot trefoil seed production. As plant maturity advances, seed yield potential increases as well as the percentage of seeds shattered (MacDonald, 1944; Anderson, 1955). In *Lotus uliginosus* (Schkuhr.), pods shatter at a rate of 10% per day, ranging from 7 to 88% seed shattering in eight days (Hare and Lucas, 1984).

The anatomical configuration of tissues in the birdsfoot trefoil pods is related to the dehiscence mechanism. Dehiscences occurs along the ventral and dorsal sutures of the carpel margins and along the median vein of the pod (Esau, 1960). Dehiscence is related to the differential moisture loss rate between parenchyma and fibrous cells (Buckovic, 1952). Dehiscence occurs when there is a change in orientation of the sclerenchyma cells and cellulose mycelles in the cell walls along with a separation of tissues that extend from the inner suture region to the outer epidermis (Fahn and Zohary, 1955). During pod moisture loss, pod valve tension is exercised by a shrinkage gradient between opposing exocarp and mesocarp tissue layers that force the pod sutures to separate (Buckovic, 1952; Fahn and Zohary, 1955). The oblique arrangement of the fibrous cells (Buckovic, 1952) is responsible for the helicoidal bending of the valves (Roth, 1977). Pod dehiscence in birdsfoot trefoil is associated with the degree of mesocarp lignification (Yang et al., 1990).

Stages of pod development have been described based on changes in pod color. The pod color can vary from dark-green or dark-green-purple to green-white and then to golden-brown (MacDonald, 1944; Anderson, 1955; Winch and MacDonald, 1961). Three physiological stages of pod and seed development have been characterized by Winch and MacDonald (1961): (i) pod elongation, where there is an increase in pod length, seeds are immature seeds, pod color is dark-green, and there is a high moisture content; (ii) seed development, seed size, pod diameter, and rate of germination increase, pod pods become light-green in color, and no dehiscence occurs; (iii) seed maturation, maximal germination percentage is reached, pod color changes to golden-brown, the pod moisture content decreases from 65 to 25%, and seed shattering is initiated. Maximal seed yield is obtained during the seed maturation stage.

Relative humidity is considered the most critical factor influencing pod dehiscence and seed shattering (Anderson, 1955; Metcalfe et al., 1957). Mature pods shatter freely when relative humidity is below of 40% (Anderson, 1955). At low temperatures and high relative humidity, the rate of shattering is less than at high temperatures and lower relative humidity (Metcalfe et al., 1957; McGraw and Beuselinck, 1983). Pod moisture content is influenced by ambient relative humidity which is a critical factor that determines when pods will dehiscence. The critical pod moisture percentage for shattering is between 10.1 and 10.4% (Metcalfe et al., 1957). Under sunny conditions, pod temperature can be 5° C higher than the ambient air temperature, resulting in a change in the relative humidity at the surface of the pod (Metcalfe et al., 1957). The moisture equilibrium between pods and the atmosphere is the primary factor responsible for pod dehiscence at a given relative humidity. Gershon (1961) found no correlation between relative humidity and pod dehiscence in birdsfoot trefoil plants grown under greenhouse conditions, but found these factors correlated when plants were grown under field conditions. This is likely due to humidity differences between these two kinds of environments (Grant, 1996).

The rate of shattering increases as the rate of water loss from the pods increases, but pods do not shatter as readily when pod drying proceeds slowly (Buckovic, 1952). Although dependent upon environmental conditions, when desiccants and plant growth regulators are used to manage vegetative growth, seed shattering can be reduced and seed yield increased (Wiggans et al., 1956). These findings suggest that factors other than relative humidity and pod moisture content alone may modify the pod shattering response. Summations of average daily temperatures have been used to explain when pod dehiscence and shattering will occur (Gataric et al., 1990).

Harvest management practices suggested to reduce yield losses due to seed shattering include: harvest desiccants (Buckovik, 1952; Cooper and Corns, 1952; Wiggans et al., 1956), early-season clipping to delay flowering (MacDonald and Winch, 1957), misting of maturing pods (Hughes, 1982), and harvest timing (Anderson, 1955). None of these have been demonstrated to consistently increase seed yield.

Grant (1996) suggests that harvest timing is the only partially effective method to reduce seed loss from shattering. Estimates for proper harvest time has been based on the rate of appearance of the pods and pod color (Anderson, 1955, Winch and MacDonald, 1961; Hare and Lucas, 1984; Winch et al., 1985; Pieroni and Laverack, 1994) and the rate of development of reproductive structures (Li and Hill, 1989). Optimal harvest time is suggested to be when 70-78% of the pods picked at random throughout the field are mature (Winch et al., 1985). A delay in the seed harvest to allow the latest developing umbels to mature can result in a 50% decrease in seed yields (Winch and MacDonald, 1961). If harvest is delayed nine days from the time of maximal mature pod percentage, seed losses are as high as 67% (Anderson, 1955). Birdsfoot trefoil pod dehiscence and seed shattering are regulated by factors other than RH, temperature, and pod moisture. Water management may influence the time of peak seed shattering events and the rate of shattering in birdsfoot trefoil.

CHAPTER 3

BIRDSFOOT TREFOIL SEED PRODUCTION: I. CROP-WATER REQUIREMENTS AND RESPONSE TO IRRIGATION

Abstract

Forage legume seed crop reproduction can be modified by regulating soil-water availability. However, responses to water stress differ for each species, so a single optimal water management strategy is not available for all crops. The response of birdsfoot trefoil (*Lotus corniculatus* L.) grown for seed to varying levels of crop-water stress has not been described. The objectives of this research are to determine the crop-water requirements, effects of soil water availability and the optimal water management conditions for birdsfoot trefoil grown for seed. Four single-application treatments varying in water depletion percentage (30 and 60% of field capacity) and replenishment amount (50 and 100% of amount depleted), were applied in 1994 and 1995, a low-stress treatment that received two to three applications per week of the amount depleted since the last application, and a non-irrigated control applied in 1994, 1995 and 1996 on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll) near Corvallis, OR. Increasing amounts of applied water resulted in increased seasonal ET_c with plants grown under low-stress having the greatest ET_c and non-irrigated control plants the least (r = 0.91). The fraction of available soil-water used by non-irrigated plants was greatest and the LS treatment the least of all treatments. The FAWU was primarily dependent upon the depletion percentage and secondarily dependent upon irrigation replacement amount. For non-irrigated conditions, the crop-water requirement ranges from 240 to 255 mm. Soil-water conditions favorable for high vegetative development and seed yield water use efficiency are opposite. Unlike other

Unlike other forage legume seed crops, birdsfoot trefoil requires minimal or no supplemental irrigation to achieve maximal seed yield.

Introduction

Birdsfoot trefoil is a perennial forage legume used for hay, pasture and silage in the midwestern and northeastern USA and eastern Canada. It is adapted to a wide range of soil conditions and environments. Seed yield can be highly variable due to an indeterminate flowering habit that results in a high rate of seed shattering during pod maturation. The effects of soil-water availability on birdsfoot trefoil seed production are not known. Supplemental irrigation water management has been shown to achieve maximal harvestable seed yield in other forage legume seed crops.

Most research regarding birdsfoot trefoil seed production comes from studies done in the northcentral USA and southcentral Canada. There are no reports for water management on birdsfoot trefoil seed production. Most seed crop water management research comes from California (carrots, Steiner et al., 1990; cowpea, Ziska and Hall, 1983a; 1983b, Ziska et al., 1985; lima bean, Ziska and Hall, 1983b; Ziska et al., 1985). Water management research for production of forage legume seed crops has been done with alfalfa (Taylor et al., 1959; Yamada et al., 1973; Hageman et al., 1975; Beukes and Barnard, 1985; Hutmacher et al., 1991; Steiner et al., 1992), red clover (Oliva et al., 1994a, 1994b) and white clover (Zaleski, 1966; Clifford, 1985, 1986; Danyack-Deschamps and Wery, 1988; Bullita et al., 1988; Oliva et al., 1994c, 1994d).

The effect of water stress on plant growth and seed yield is different among seed crops, depending on the time when the stress occurs and the irrigation management approach. Alfalfa and white clover seed yields can be optimized by limiting crop vegetative development by controlled water stress (Clifford, 1985; 1986; Steiner et al., 1992, Oliva et al., 1994c). Red clover seed yields are optimized when water stress is avoided (Oliva et al., 1994b). Alfalfa seed crop response to irrigation management differs depending upon the frequency and amount of irrigation water applied as well as the year of production and the quantity of water applied in the winter and stored for use during reproduction in the summer (Steiner et al., 1992).

Based on leaf extension rate, birdsfoot trefoil is more water stress tolerant than white clover (Davis et al., 1994). Birdsfoot trefoil has also been demonstrated to be more drought resistance than white clover under grazing conditions in mixed pastures (Davis and Bell, 1957). The depth of root penetration is considered a vital factor related to drought resistance (Whyte et al., 1953). The success of birdsfoot trefoil in droughted habitats is also attributed to a high root-shoot ratio as well as the development of a strong deep taproot that reduces adult plant mortality (Foulds, 1978).

The objectives of this research are to determine the crop-water requirements, effects of soil-water availability, and the optimal water management conditions for birdsfoot trefoil grown for seed.

Materials and Methods

The experiment was conducted in 1994, 1995, and 1996 at the Oregon State University, Hyslop Field Laboratory near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll). The experimental area was fumigated with methyl bromide (360 kg ha^{-1}) preceding seedbed preparation to evenly control weeds. Birdsfoot trefoil 'MU-81' (Beuselinck and McGraw, 1986) was planted 30 August 1993 into a level seedbed in single rows, 0.6 m apart, and at a rate of 2.3 kg ha^{-1}. Water was applied with high-pressure overhead sprinklers just after planting and as needed the following 22 days to establish the crop.

Common commercial practices for pest control were used. Annual grasses, broadleaf weeds, and volunteer birdsfoot trefoil seedlings were controlled in winter 1994 with hexazinone at 0.56 kg ha^{-1} to control broadleaf weeds. In the winter 1995 and 1996, hexazinone was applied at a rate of 1.1 kg ha^{-1} to control weeds and volunteer birdsfoot trefoil seedlings. In spring 1995, glyphosate was applied at a rate of 5.6 L ha^{-1} by directed spray between the rows to control volunteer seedlings. The plots had the forage removed (clip-back) on 17 May in 1994, 26 May in 1995, and 4 June in 1996. Clip-back promotes uniform flowering and enhances flower development when warmer temperatures occur and insect pollinators are active. The plots were monitored for Lygus (*Lygus spp.*) and aphids (*Nearctaphis bakeri* [Cohen]) once a week during the reproductive period. All plots were sprayed in 1994 and 1996 with methoxychlor applied at the peak time of flowering at a rate of 1.7 kg ha^{-1}. No insecticide was needed in 1995. Four honey bee (*Apis mellifera* L.) hives were placed close to the experimental area each year at the time of initial bloom.

The plots were arranged in a randomized complete block design with four replications and six treatments in 1994 and 1995. Two of the six treatments were used in 1996. Each plot was 4.5 m wide by 10 m long and was surrounded by a furrow with dikes to prevent lateral surface water movement if application rates exceeded the soil-water infiltration rate. The 1-m wide alleys at the ends of each plots were also diked.

A surface trickle irrigation system delivered water to each plot through 3.5 L h^{-1} in-line, turbulent-flow emitters spaced 0.9 m apart in five plastic drip lines 60 cm apart and placed perpendicular to the planting rows. A distribution manifold consisting of a mesh filter, ball valve, residential water flowmeter, volumetric controller, and a pressure regulator allow water to be applied to all four replications of each treatment at the same time.

For 1994 and 1995, five supplemental irrigation treatments were applied between the period from clip-back to seed harvest. The treatments were: (i) low-stress (LS), the soil-water content was maintained close to 100% field capacity (FC) by two or to three water application replacements per week during the period from early-June until three weeks before seed harvest based on neutron attenuation soil-water content measurements; (ii) single water replacement to 50% FC when soil-water depletion was 30% (D30-F50); (iii) single water replacement to 100% FC when soil-water depletion was 30% (D30-F100); (iv) single water replacement to 50% FC when soil-water depletion was 60% (D60-F50); (v) single water replacement to 100% FC when soil-water depletion was 60% (D60-F100); and (vi) a non-irrigated control (C). In 1996, only treatments LS and C were evaluated. Besides these treatments, two extra plots were maintained adjacent to the experimental area for destructive flower sampling during the reproductive period. These plots received water management treatments (i) and (vi).

Changes in volumetric soil-water content of each plot were monitored weekly until harvest by neutron attenuation (Cuenca, 1988). One aluminum access tube 5.3 cm internal diameter and 3 m long was installed in the center of each plot after planting. Measurements were taken 48 h after each irrigation at depths of 0.45, 0.65, 0.95, 1.25, 1.55 and 2.0 m below the soil surface.

Local condition calibration of the neutron attenuation probe for volumetric soil-water content (VWC) was done with available data based on gravimetric data and an average soil bulk density value of 1.35 Mg m^{-3} for the research area (Oliva, 1992) using the equation:

$$VWC = -21.4 + 48.39\ CR \qquad [1]$$

where CR is the neutron attenuation count ratio. The estimated VWC values were subtracted from the permanent wilting point value and used to calculate the available soil-water content per depth of soil:

$$AW_i = (VWC_i - PWP)\ D_i \qquad [2]$$

where VWC_i = volumetric soil-water content of the i^{th} sample measured by neutron attenuation, PWP = permanent wilting point (0.22 m^3 m^{-3}; Oliva et al., 1994a), and D = active soil profile depth; and the total available water (TWA):

$$TAW = (FC - PWP)\ D \qquad [3]$$

where field capacity (FC) equals 0.46 m^3 water m^{-3} soil (Oliva et al., 1994a); and the fraction of available soil-water used (FAWU) was estimated as described by Oliva et al., (1994a, 1994c):

$$FAWU_i = 1 - (AW_i\ TAW^{-1}), \qquad [4]$$

where $FAWU_i$ = fraction of available soil-water used of sample *i*, AW_i = available soil-water of sample *i* in mm, and TAW = total available soil-water.

Seasonal estimated crop evapotranspiration (ET_C) was determined as the sum of applied water, precipitation, and the change in soil-water content estimated by neutron attenuation. Based on the neutron attenuation readings at the deepest depths throughout the cropping season, it was assumed no deep percolation occurred in 1994 and 1995. Because of plant mortality during the winter of 1995-1996 and excessive estimated ET_C in the LS treatment in 1996, drainage through the soil profile through root channels was presumed. The estimated seasonal ET_C for the LS treatment in 1996 was adjusted for presumed drainage by determining the functional relationship between pan evaporation (E_p) and seasonal ET_C for all treatments and years excluding LS in 1996 and substituting this value for the one determined by the change in soil-water content:

$$ET_C = -324.4 + 1.25\ E_p \qquad [5]$$

$$r^2 = 0.91;\ P \leq 0.0001$$

Seasonal crop reference evapotranspiration (ET_r) was calculated from Class A evaporation pan measurements (E_p) obtained 400 m from the trial site and using a correction factor coefficient (f_i) for different groundcover, levels of mean relative humidity, and 24-h wind run (Doorenbos and Pruit, 1977):

$$ET_r = E_p f_i \qquad [6]$$

where f_i = 0.730, 0.735, and 0.735 in 1994, 1995, and 1996, respectively.

Average daily ET_C and ET_r were calculated by dividing seasonal ET_C and ET_r, respectively, by the crop season length in days. The crop coefficient (k_C) is the ratio between seasonal ET_C and seasonal ET_r:

$$k_C = ET_C\, ET_r^{-1} \qquad [7]$$

Accumulated soil-water depletion at each depth was calculated for LS and C treatments as the sum of the differences in the changes of the volumetric soil-water content (VWC) at the vegetative, reproductive, and maturation plant development stages. The vegetative stage encompassed the period from time of clipback until to initial flowering; reproductive stage was from initial flowering to initial pod development; and maturation from initial pod development to time of seed harvest.

To determine the plant water-stress status, a Scheduler (Plant Stress Monitor, Carborondum Co. Solon, OH) was used to measure crop canopy temperature (T_c), air temperature (T_a), and water vapor pressure deficit (VPD). Five measurements were taken at least once a week in all plots from 24 June (DOY 175) to 25 August (DOY 237) in 1994, from 17 July (DOY 198) to 25 August (DOY 237) in 1995, and from 5 July (DOY 186) to 22 August (DOY 234) in 1996, on clear, cloud-free days, between 1200 to 1400 h. Measurements were taken 1 m from the top of the canopy at a 45° oblique angle facing northwest from the shorter west-east axis of each plot.

A crop water stress index (CWSI) was estimated as described by Idso et al. (1981a). The CWSI is a simple criterion for identifying potential evaporation state and is used to estimate the soil-induced plant-water stress and is based on the relationship between the canopy-air temperature differential (T_C-T_a) and the VPD of the air. The CWSI measurements range from 0 to 1. The measured temperature differentials are scaled to the maximum expected difference between low-water-stressed conditions (treatment LS) and stressed conditions (treatment C). The scaled values are normalized for environmental variability using the VPD of the air (Idso et al., 1981a).

Data obtained from the LS treatment were used to estimate the nonstressed baseline for the T_c-T_a and VPD relationship, and the stressed baseline was determined based on theory as being 4.5°C (Idso et al., 1981b). Average seasonal CWSI values were calculated as the mean of weekly CWSI values for the seed production period (Oliva et at., 1994a; 1994c).

The effect of inflorescence density on canopy temperatures and calculated CWSI values during pre-peak and post-peak of flowering was determinated each year. Measurements were made in 1994 on DOY 201 and 213; 1995 on DOY 201, 206 and 221; and 1996 on DOY 192, 203, and 207. Plants in 0.2 m^2 sections of the extra plots adjacent to the main experimental area had 0, 25, 50, 75 and 100% of the inflorescences displayed sequentially removed by hand. Scheduler readings were taken using the same methodology indicated above but keeping the target inside the different inflorescence density sample areas.

Leaf water potential (Ψ_L) was determined in 1995 and 1996 using a pressure chamber (Scholander et al., 1965). Stem sections containing four or five trifolioliate leaf clusters were sampled at random weekly from every plot between 1300 and 1500 h. The sampled stem sections were wrapped in plastic film before excision to minimize water loss errors from the time of sampling until the measurements were made (Leach et al., 1982).

The plots were harvested for seed yield when the most mature pods were light tan to brown colored and shattering. Details of the harvest and seed cleaning methods are given in Chapter 4. Total above-ground phytomass

(TAGP) and harvested seed yield (SY) water-use efficiencies were calculated as a function of dry matter weight per water volume of ET_c.

Pearson correlation coefficients were determined among all water inputs and measured soil and plant variables. Because of the high degree of collinearity among the measured variables, multivariate common factor analysis was used to determine the independence of different groupings of variables (Hair et al., 1995). Factor rotation was by the equimax rotation method.

Regression analyses were performed to determine relationships between canopy-air temperature differential with VPD and for Ψ_L with CWSI. Standard errors of the mean were estimated for VWC and FAWU. Student's *t* pairwise comparison were used to contrast crop-water use efficiencies between years in 1994 and 1995 and between treatments LS and C in 1996. The general linear test approach was used to determine whether two regression lines were identical (Neter and Wasserman, 1974). Spearman's rank correlation test (Snedecor and Cochran, 1980) was used to determine if any differences existed in the rankings of CWSI and FAWU and TAGP and SY water use efficiencies by irrigation treatments. All variables were tested by analysis of variance and mean differences determined by Fisher's protected LSD at $P \leq 0.05$.

Results and Discussion

Crop evapotranspirative demand

The time of irrigation initiation for LS treatment was the same every year (8 June, 8 June and 7 June in 1994, 1995 and 1996, respectively). However, the soil-water content at LS treatment initiation time was different each year because of different amounts of spring precipitation. In 1994, 165 mm of precipitation were received from March to May and by the time of clip-back, 16% of the available soil-water was depleted. For the same period in 1995 and 1996, 290 and 316 mm of precipitation was received, and 11 and 20% of the soil-water was depleted, respectively. Initiation time of the single water application treatments in 1995 were delayed until the levels of soil-water depletion were similar to those in 1994. The 1995 crop season length was shorter than 1994, and the 1994 season was shorter than 1996 (Table 3.1).

There were no differences among years in seasonal or average daily ET_c values across the range of all treatments ($P \leq 0.58$). Increasing amounts of applied water resulted in increased seasonal ET_c ($r = 0.91$; $P \leq 0.0001$). Similar relationships between amount of applied water and seasonal ET_c are found for red clover ($r = 0.92$; $P \leq 0.0001$) and white clover ($r = 0.83$; $P \leq 0.001$) (Oliva et al., 1994a and 1994c). Since accumulated seasonal ET_c depends on the length of the cropping season, average daily ET_c provides a better estimator of water use differences among irrigation treatments (Oliva et al., 1994a; 1994c). The plants grown under LS had greater ET_c than all other treatments and the control plants had generally the least ET_c among all treatments (Table 3.1). There were no differences among years for ET_c. Average daily ET_r was constant among treatments, but differed among years ($P \leq 0.001$). Regardless of yearly environmental differences, birdsfoot trefoil responded similarly to different levels of soil-water availability in different years.

The crop coefficient value for the LS treatment was generally greater than the rest of the treatments in all years, indicating that the plants were subjected to the least amount of stress of all treatments (Table 3.1). Only for the LS treatment in 1994 did the crop coefficient approach the 1.05 value reported for clover pasture crops (Doorenbos and Pruit, 1977). All other treatments had crop coefficient values less than 1.0 which indicates that limited soil-water was available to the plants at different times during the reproductive development period. Similar findings were found for white clover (Oliva et al., 1994c). The

Table 3.1. Crop season length, seasonal crop water stress index (CWSI), seasonal fraction of available soil-water used (FAWU), change in soil water content, precipitation, applied water, seasonal estimated crop evapotranspiration (ET_c), pan evaporation, seasonal reference evapotranspiration (ET_r), and crop coefficient for six birdsfoot trefoil seed irrigation treatments in 1994 and 1995, and two treatments in 1996.

Treatment	Crop season length	Seasonal CWSI	Seasonal FAWU	Change in soil water[†]	Precipitation	Applied water	Seasonal ET_c[‡]	Pan evaporation[¶]	Seasonal ET_r[#]	Crop coefficient[††]
	d			----------	----------	mm	----------	----------	----------	
Year 1994										
LS	100	0.12	0.09	62	55	320	437	591	432	1.01
D30-F50	83	0.52	0.35	182	55	48	284	486	355	0.80
D30-F100	85	0.38	0.28	156	55	91	302	500	365	0.83
D60-F50	84	0.44	0.32	135	55	86	276	493	360	0.77
D60-F100	85	0.30	0.25	72	55	179	306	500	365	0.84
C	78	0.64	0.38	190	55	0	246	458	334	0.74
Year 1995										
LS	95	0.10	0.03	2	93	256	351	560	412	0.85
D30-F50	77	0.43	0.22	165	75	41	281	464	341	0.82
D30-F100	85	0.40	0.22	134	87	92	314	502	369	0.85
D60-F50	78	0.51	0.33	73	75	91	239	469	345	0.69
D60-F100	82	0.49	0.24	8	75	190	273	492	362	0.76
C	74	0.57	0.35	166	74	0	240	446	328	0.73
Year 1996										
LS	83	0.19	0.15	91	48	199	338	530	390	0.87
C	72	0.51	0.55	207	48	0	255	457	336	0.76

Table 3.1. Continued.

† Data shown are soil water net change in total active profile (1.25 m deep in 1994 and 1995, and 1.60 m deep in 1996).

‡ Seasonal ET_c = irrigation water + precipitacion + crop season-soil water content changes during the crop season.

§ Estimated as the ratio of the seasonal value with crop season length (d).

¶ Data from a class A evaporation pan.

Seasonal reference evapotranspiration (ET_r) = pan coefficient * pan evaporation. Pan coefficient is a function of relative humitidy, wind speed and pan-surrounding environment.

†† Crop coeffcient = estimated ET_c / seasonal ET_r. Crop coefficient is most closely computed by treatment LS. All other treatments represent coefficient values that indicate limited soil-water availability and its usefullness is to compare differences among years and within treatments.

early replacement irrigation treatments (D30-F50 and D30-F100) have crop coefficient values more similar to the LS treatment than the later replacement irrigation treatments (D60-F50 and D60-F100). The later treatments are more similar to the non-irrigated control. Plants grown in non-irrigated conditions generally have the lowest crop coefficient values. These results indicate that water stress is reduced for plants grown under LS, D30-F50, and D30-F100 conditions compared to those for the D60-F50, D60-F100, and during the initial stages of reproductive development (Chapter 4).

Soil-water depletion

The changes in volumetric soil-water content from different soil depths varied depending on the year of production and irrigation treatment (Fig. 3.1, only treatments LS and C are shown). No deep percolation occurred from the time of clip-back until seed harvest in the 1994 and 1995 water balance computations. In 1996, based on the excessive ET_c value in LS treatment, drainage is presumed to have occurred through root channels due to plant mortality in winter 1995-1996.

In the non-irrigated control treatment from the time of clip-back to initial flowering (vegetative period), the greatest amount of soil-water was utilized from the upper 1.25 m of the soil profile in 1994 and 1996 (Fig. 3.2). Precipitation amounts in June were greatest in 1995 compared to 1994 and 1996 (60, 48, 22 mm, respectively) which reduced the need for plant water uptake from the soil during the vegetative period in 1995. During the plant flowering stage, most soil-water was taken up from the upper 1.25 m of the soil profile in 1994 and 1995. However in 1996, water was taken up from as deep as 2.0 m, indicating the plant root zone had continued to descend. From the time of initial pod development until seed harvest (pod filling), water was depleted rather uniformly from all soil depths.

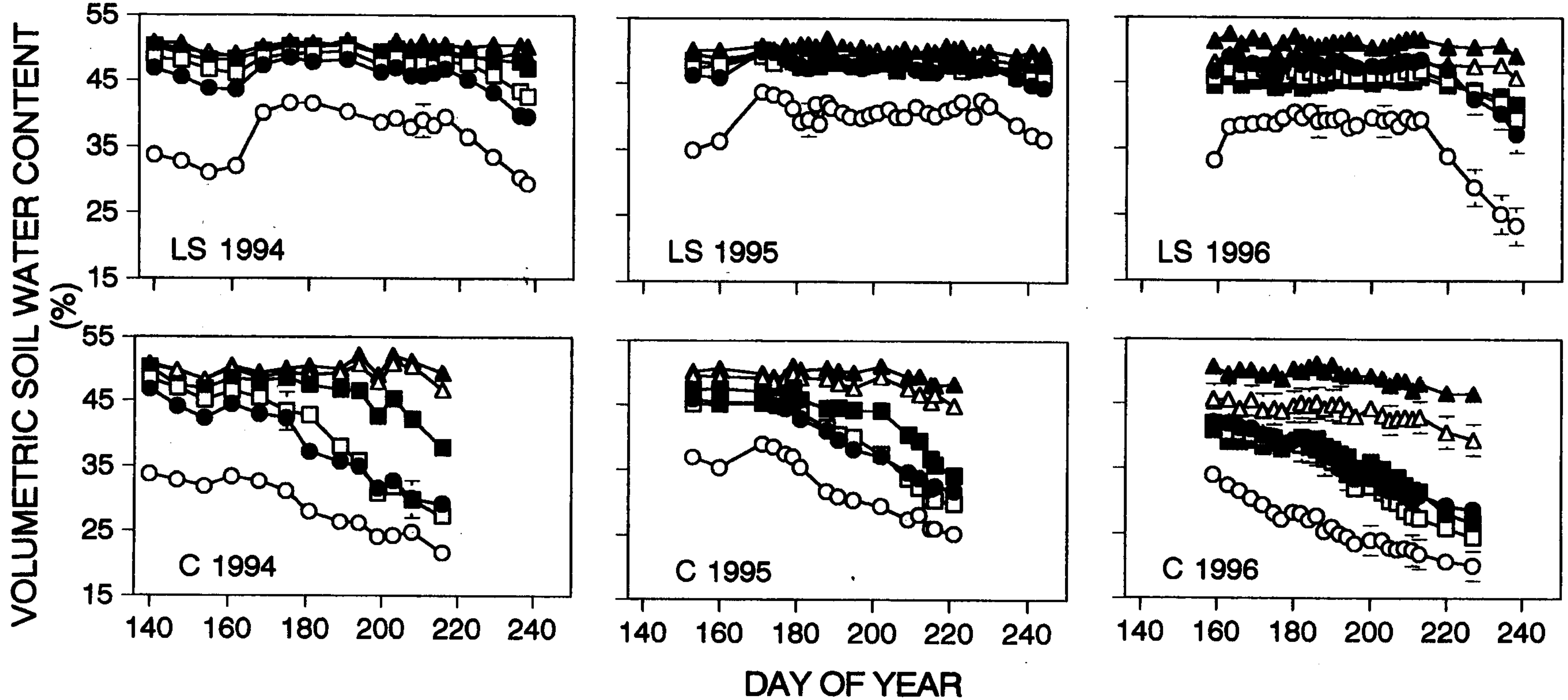

Fig. 3.1. Variation of volumetric soil-water content throughout birdsfoot trefoil seed crop growing season for low-stressed (LS) and non-irrigated (C) treatments in 1994, 1995, and 1996. Graph symbols ○, ●, □, ■, △, and ▲ indicate soil depths at 0.45, 0.65, 0.95, 1.25 1.60, and 2.00 m, respectively. Vertical bars indicate standard error of the mean.

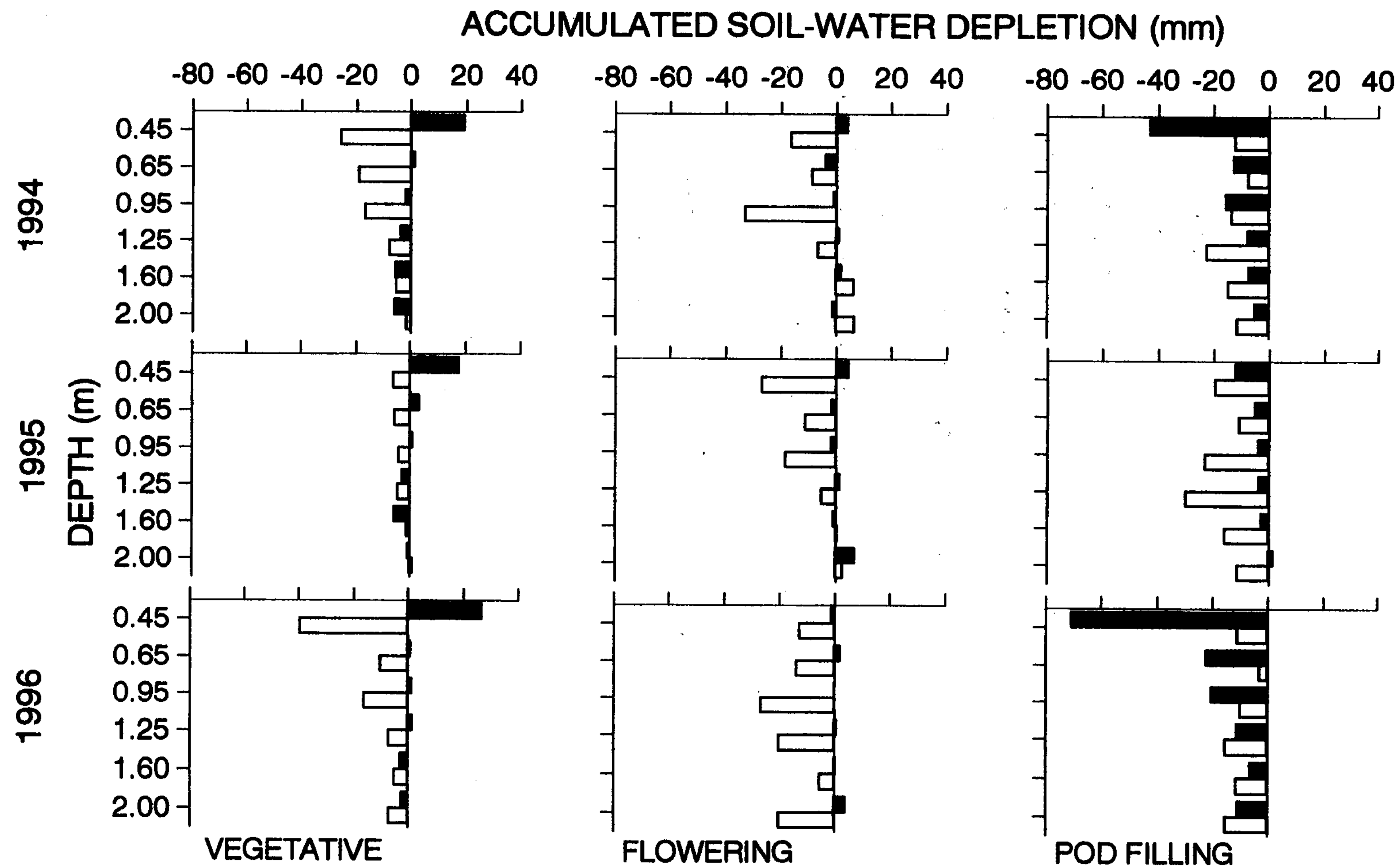

Figure 3.2. Accumulated soil-water depletion at six soil depths for three crop development periods for low stressed (■), and non-irrigated (□) birdsfoot trefoil seed irrigation treatments in 1994, 1995, and 1996. Vegetative, flowering, and pod filling stages occurred from DOYs 138 to 188, 181 to 211, and 202 to 238, respectively.

In contrast, the LS treatment plants accumulated water (positive values) above 0.45 m from the soil surface during the vegetative period in all three years. The rest of the soil depths are maintained at approximately field capacity during the vegetative period as well as during the flowering stage of development. During the pod filling stage, the soil-water content in the LS treatments is largely depleted. This results from ceasing water applications. The number of days from the end of water application until seed harvest are 25, 15, and 27 for 1994, 1995, and 1996, respectively. The fewer number of days without irrigation until harvest in 1995 may account for the relatively lower amount of water extracted from the soil profile compared to 1994 and 1996. It appears that the over-estimation of the ET_c and resulting excessive applications of water to the LS plots in 1996 had no effect on the soil-water uptake profiles. The active root zone for birdsfoot trefoil is greater than that of white clover (Oliva et al., 1994c) and equals or exceeds that of red clover (Oliva et al., 1994a).

The utilization of stored available soil-water by the crop is dependent upon the frequency of water application and the amount replaced after depletion. The FAWU values for the non-irrigated control treatment is greatest and the LS treatment the least (Table 1). The FAWU is primarily dependent upon the depletion percentage and secondarily dependent upon irrigation replacement amount. The D60-F50 has a higher FAWU than D30-F50. The FAWU for D30-F100 and D60-F100 are similar and greater than that of LS.

Crop water stress index and leaf water potential

Two low-stressed CWSI baselines are related to plant development stages before and after the time of peak flowering in all three years (Fig. 3.3). The two nonstressed CWSI baseline functions have equal slopes but the

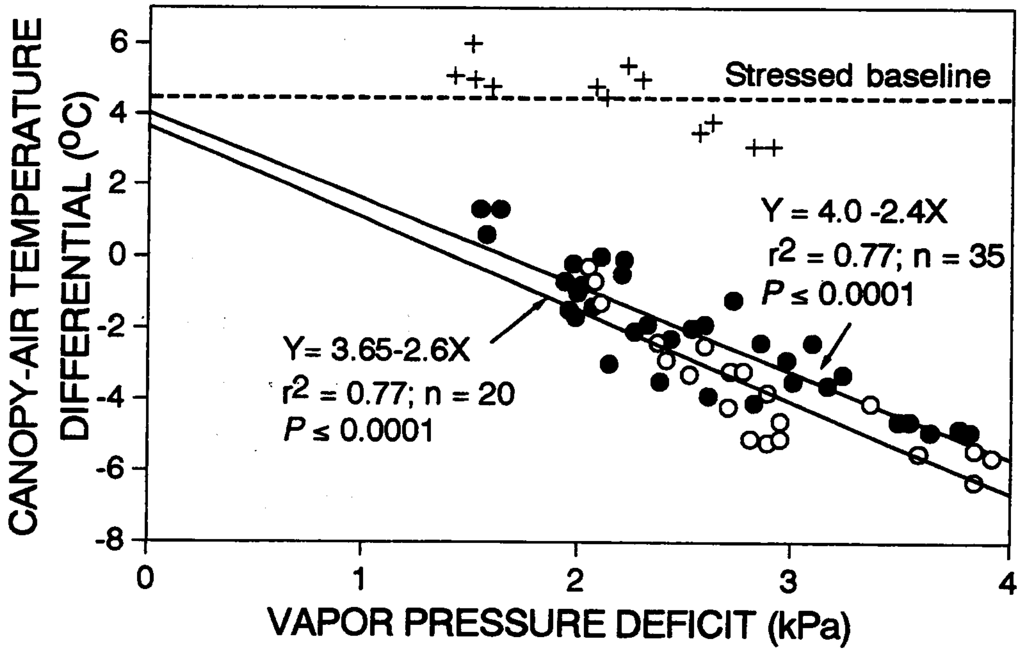

Fig. 3.3. Relationships of crop water stress index non-stressed baselines for canopy minus air temperature differential as a function of water vapor pressure deficit from the low-stress treatment before (○) and after (●) peak flowering of birdsfoot trefoil grown for seed in 1994, 1995, and 1996. The upper line is based on the non-irrigated control treatment (+) at the end of each crop growing season.

in-season change in non-stressed baseline position is the result of differences in canopy temperature measurements obtained before and after peak of flowering that are the result of flower density differences. Similar findings of changes in non-stressed baseline position due to changes in plant morphological stage have been reported for alfalfa (Hutmatcher et al., 1991), red clover (Oliva et al., 1994a), and white clover (Oliva et al., 1994b).

The T_c-T_a differential value for birdsfoot trefoil (4.5° C, Fig. 3.3) is lower than those for red and white clover which are approximately 10° C (Oliva et al., 1994a and 1994c, respectively). Both red clover and white clover have larger succulent leaves than birdsfoot trefoil and may have lower rates of transpiration due to greater stomatal resistance induced by water stress. Birdsfoot trefoil is better adapted for growth under water stress than white clover (Davis et al., 1994). This may be due to birdsfoot trefoil having a lower growth rate than other species which are not as well adapted to growth under stressed conditions (Grime et al., 1988).

The most negative Ψ_L values for birdsfoot trefoil in 1995 and 1996 are -1.2 and -0.72 MPa, respectively. This differs substantially from values reported for the forage legume seed crops alfalfa (-4.0 MPa, Hutmacher et al., 1991), red clover (-2.0 MPa, Oliva et al., 1994a) and white clover (-2.5 MPa, Oliva et al., 1994c). Plants of birdsfoot trefoil grown for forage in July under irrigated conditions in Minnesota had Ψ_L values that ranged from -0.1 to -0.4 MPa (Peterson et al., 1992) which are similar to those measured in this study under both LS and non-irrigated conditions. Non-irrigated plants in Minnesota had Ψ_L values that ranged from -1.6 to -3.6 MPa which are greater than those measured in this study.

The relationship between birdsfoot trefoil Ψ_L and CWSI for the LS and non-irrigated treatments is significant but not of practical value because of the low percentage of total variation accounted for by the regression functions (r^2 = 0.32; $P \leq 0.001$ in both 1995 and 1996). The relationships between Ψ_L and

CWSI reported for alfalfa (r^2 = 0.91, Hutmatcher et al., 1991), red clover (r^2 = 0.75, Oliva et al., 1994a) and white clover (r^2 = 0.74, Oliva et al., 1994c) varied and may be related to the general environmental conditions in which the experiments were conducted. The alfalfa study was conducted in an arid conditions of central California where day-time temperatures commonly exceeded 35° C. Average Minnesota temperatures were 25° C. Average temperatures in western Oregon in July are 20° C. This suggests that effective relationships between Ψ_L and CWSI measurements for birdsfoot trefoil are obtained when day-time temperatures are greater than those in western Oregon.

The low CWSI and Ψ_L values determined in 1995 and 1996 indicate that birdsfoot trefoil is well adapted to growth under water stress conditions due to its ability to take up water from deep soil depths and a low growth rate that requires a low crop evaporative demand. The CWSI for the non-irrigated control treatment is generally greater and the LS treatment generally lower than the single water application treatments. The CWSI values do not differ among years. The LS and C Ψ_L values throughout the season are correlated with CWSI in both 1995 and 1996 (r = -0.77 and -0.9, respectively, $P \leq 0.05$).

Leaf water potential is not as useful a measure as CWSI of birdsfoot trefoil plant-water status under the conditions of this experiment. The primary disadvantage of the CWSI is that it must be used on free-cloud days with low wind speeds and within a relatively narrow time period (Gardner et al., 1992). These restrictions are not always met during the summer in western Oregon.

Plant water use efficiency

Total above-ground phytomass (TAGP) water use efficiency did not differ among all treatments in 1994 (Table 3.2).

Table 3.2. Total above-ground phytomass and seed yield water use efficiencies for six birdsfoot trefoil seed irrigation treatments in 1994 and 1995, and two treatments in 1996.

Treatment	Total non-reproductive phytomass water-use efficiency†			Seed yield water-use efficiency†		
	1994	1995	1996	1994	1995	1996
	kg ha^{-1} mm^{-1} ET_c					
LS	21.7 a‡	27.0 a	25.4 a§	0.4 c	0.4 b	0.6 b§
D30-F50	19.3 a	20.7 b		1.8 b	1.1 a	
D30-F100	21.6 a	23.7 ab		1.8 b	0.9 a	
D60-F50	21.3 a	25.1 a		2.7 a	1.2 a	
D60-F100	19.2 a	25.5 a		2.6 a	1.2 a	
C	20.5 a	20.5 b	19.6 b	2.8 a	0.9 a	1.0 a

ns, *, **, *** Not significant, significant at $P \leq 0.05$, 0.01, and 0.001, respectively.

† Water-use efficiency expressed as the ratio of the component with the estimated seasonal crop evapotranspiration (ET_c).

‡ Values within columns followed by a different letter are significantly different according to Fisher's protected LSD test at $P \leq 0.05$.

§ Ratio estimated considering 338 mm as adjusted ET_c.

The TAGP is greater for LS than the non-irrigated C treatment in 1995 and 1996. Among the single water application treatments, only the D30-F50 has a lower TAGP water use efficiency than LS. The effect of the irrigation treatments on seed yield water use efficiency is different from that of TAGP water use efficiency. In all years, LS has the lowest and the non-irrigated control the greatest seed yield water use efficiency. In 1994, the two 30% depletion irrigation treatments (D30-F50 and D30-F100) are not as efficient as the 60% depletion treatments and the non-irrigated control. This is because the plants irrigated at 30% depletion are under less stress early in the growing season because of the early water application. These plants have to rely more on soil-water availability to sustain reproductive development in the late season than do plants grown in the 60% depletion treatments. This influences not only seed yield water use efficiency, but also flower development and total seed yield (Chapter 4). In 1995, all single irrigation treatments have the same seed yield water use efficiencies as the non-irrigated control.

These findings suggest that soil-water conditions that are favorable for high TAGP and SY water use efficiency are opposite ($r_s = -0.55$; $P \leq 0.05$). The birdsfoot trefoil plants very efficiently utilize any applied water and convert it into TAGP. As the amount of irrigation water applied is increased, the TAGP water use efficiency increases ($r = 0.54$; $P \leq 0.05$). Seed yield water use efficiency is not related to the total amount of applied water ($r = -0.16$; $P \leq 0.59$), but rather the general conditions of the environment that affect crop-water stress as indicated by average ET_r ($r = -0.60$; $P \leq 0.02$). Water applied during initial reproductive development increases vegetative production at the expense of seed yield (Chapter 4).

Relationships among plant, soil, and water variables

There is a high degree of collinearity among the crop, soil, and water variables indicated by the numerous significant correlations (Table 3.3). Factor analysis is used to separate the effects of the different variables into three components that describe 89.2% of the variation among the inputs and outputs within the birdsfoot trefoil seed production system (Table 3.4). The three components are named after the primary variable that is independently and most strongly associated with that component.

The first factor describes plant biological processes that are related to estimated crop evapotranspiration (average ET_c, crop coefficient, and total ET_c). These three variables are not associated with the other two factors. The crop coefficient (k_c, equation 7) is correlated with values of ET_c and not ET_r because there are significant irrigation treatment differences for ET_c values but not for ET_r. The second factor relates to changes in the soil-water percentage that is independent of the crop evapotranspiration variables. Precipitation amount during the reproductive period is weakly associated ($P \leq 0.12$) with soil-water change and not associated with any other variables. The third factor is described by the average daily ET_r which is the result of physical processes unrelated to the biological birdsfoot trefoil variables.

The remaining variables describe associations between the evapotranspiration estimators and changes in soil-water content. Changes in soil-water content are dependent upon the pre-established irrigation treatments thresholds. Neutron attenuation measurements are used to determine the FAWU and amount of applied water that needs to be applied. Since soil-water depletion is dependent upon plant evapotranspiration, there is a linkage between soil-water changes and evapotranspiration by pan evaporation which is used to determine ET_r (equation 6). The CWSI is an independent measure of crop response to soil-water availability that depends upon the differential between crop canopy and ambient air temperature (Idso et

Table 3.3. Pearson correlation coefficients among crop, soil, and water variables affecting birdsfoot trefoil seed production.

Variable	Variable					
	D-ET_c	D-ET_r	k_c	CWSI	FAWU	Season
Daily ET_r (D-ET_r)	.218					
Crop coefficient (k_c)	.949	.098				
Crop water stress index (CWSI)	-.830	-.049	-.824			
Fraction available water used (FAWU)	-.625	.217	.693	.833		
Season length (Season)	.537	-.424	.677	-.767	-.776	
Soil-water change (SWC)	-.271	.097	-.305	.629	.735	-.689
Precipitation (Precip)	-.166	-.220	-.119	-.090	-.422	.202
Water applied (Water)	.690	-.092	.734	-.879	-.837	.858
Season-long ET_c (S-ET_c)	.915	-.114	.968	-.894	-.776	.812
Pan evaporation (Pan)	.798	-.152	.861	-.918	-.822	.901
Season-long ET_r (S-ET_r)	.801	-.122	.854	-.924	-.831	.895
	SWC	Precip	Water	S-ET_c	Pan	
Precipitation (Precip)	-.432					
Water applied (Water)	-.853	.123				
Season-long ET_c (S-ET_c)	-.478	-.028	.853			
Pan evaporation (Pan)	-.645	.052	.929	.957		
Season-long ET_r (S-ET_r)	-.661	.079	.933	.953	.999	

Table 3.4. Common factor analysis of crop, soil, and water variables affecting birdsfoot trefoil seed production.

Variable	Factor 1	Factor 2	Factor 3
	---------- Rotated factor loadings†		------------
Crop coefficient	**.980**	.073	.068
Average ET_c	**.963**	.259	.070
Total ET_c	**.950**	.054	-.236
Pan evaporation	**.863**	**.455**	.084
Total ET_r	**.853**	**.481**	.056
CWSI	**-.816**	**-.478**	.110
Water applied	**.710**	**.652**	-.003
FAWU	**-.607**	**-.684**	-.152
Soil-water change	-.246	**-.932**	.004
Precipitation	-.185	**.528**	.186
Average ET_r	.021	-.098	**-.986**
Explained variation (%)	53.6	25.4	10.2

Bold numbers indicate significance at $P \leq 0.05$.

† Factor loadings by equimax rotation method.

al, 1981a). The CWSI measurement is remotely sensed and does not depend on estimates of soil-water content (soil-based measures) or estimates of ET_c to calculate its value.

The FAWU increased with time until irrigation water was applied (Fig. 3.4). The ranking irrigation treatments by FAWU and CWSI values are similar ($r_s = 0.88$; $P \leq 0.0001$). In general, as soil-water is depleted through plant transpiration, the trend of CWSI increases are similar as the pattern of FAWU, but tended to be lower before the peak of flowering and higher afterwards. The CWSI values also tended to increase faster than FAWU as the cropping season progressed. Deviations in CWSI values from FAWU in 1995 for treatments D60-F50 and D60-F100 are due to short-term in-season temperature increases (DOY 212, Fig 3.4) that are detected by CWSI measurement but not the soil-based measurement by neutron attenuation that is used to determine FAWU. The CWSI values tended to decrease at the end of the cropping season in 1995 as temperatures decreased or precipitation occurred.

Birdsfoot trefoil grown for seed requires minimal or no supplemental irrigation. For non-irrigated conditions, the crop water requirement ranges from 240 to 255 mm (Table 3.1). The seed crop-water requirement to meet high evaporative demand for the best irrigation treatment is approximately 275 mm. This is only 20 mm more than the amount required for non-irrigated conditions and indicates the inefficiency of irrigating birdsfoot trefoil grown for seed.

Conclusions

Increasing amounts of applied water results in increased seasonal ET_c. Plants grown under low stress have greater ET_c than all other treatments and the non-irrigated control plants generally the least ET_c among all treatments. There are no differences among years for ET_c. Average daily ET_r is constant

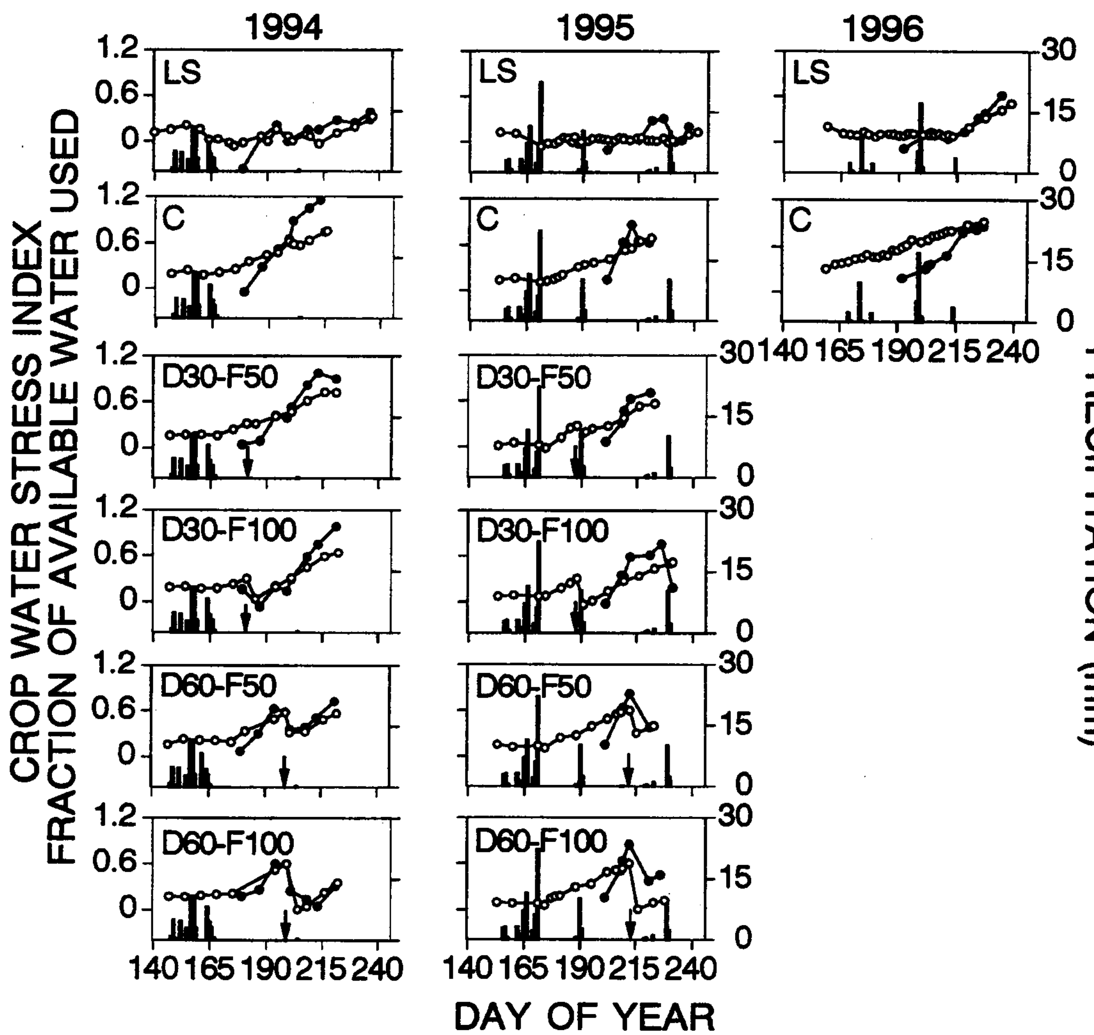

Fig. 3.4. Crop water stress index (●) and fraction of available soil-water used (○) for six birdsfoot trefoil seed irrigation treatments in 1994 and 1995, and two treatments in 1996. Treatments are indicated in the upper left-corner of each graph. Bar graphs, arrows ↓ , and vertical bars indicate daily precipitation, time of irrigation application (not shown for treatment LS), and standard error of the mean, respectively.

among treatments, but differed among years. Regardless of yearly environmental differences, birdsfoot trefoil responds similarly to different levels of soil-water availability in all three years.

The pattern of soil-water depletion from different soil depths varies by irrigation treatment and year of production. The utilization of stored available soil-water by the crop is dependent upon the frequency of water application and the amount replaced after depletion. The fraction of available water used values for the non-irrigated control treatment is greatest and the LS treatment the least. The FAWU is primarily dependent upon the treatment depletion percentage level and secondarily dependent upon irrigation treatment replacement amount.

Two low-stressed crop water stress index baselines are related to plant development stages before and after the time of peak flowering in all three years. The two non-stressed CWSI baseline functions have equal slopes but the in-season change in non-stressed baseline position is the result of differences in canopy temperature measurements obtained before and after peak of flowering that are the result of flower density differences. The relationship between birdsfoot trefoil leaf-water potential and CWSI for the low stress and non-irrigated treatments is significant but not of practical value because of the low percentage of total variation accounted for by the regression functions.

Soil-water conditions that are favorable for high total above-ground phytomass and seed yield water use efficiency are opposite. Birdsfoot trefoil plants very efficiently utilized applied water and convert it into TAGP. As the amount of irrigation water applied is increased, the TAGP water use efficiency increases. Seed yield water use efficiency is not related to the total amount of applied water, but rather the general conditions of the environment that affect crop-water stress as indicated by average ET_r.

Unlike other forage legume seed crops, birdsfoot trefoil grown for seed requires minimal or no supplemental irrigation. For non-irrigated conditions, crop water requirement ranges from 240 to 255 mm. The seed crop-water requirement to meet high evaporative demand is approximately 275 mm. This is only 20 mm more than the amount required for non-irrigated conditions and indicates the inefficiency of irrigating birdsfoot trefoil grown for seed.

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CHAPTER 4

BIRDSFOOT TREFOIL SEED PRODUCTION: II. PLANT WATER STATUS ON REPRODUCTION AND SEED YIELD

Abstract

Forage legume seed crop reproduction can be modified by regulating soil-water availability. However, responses to water stress differ for each species, so a single optimal water management strategy is not available for all crops. The response of birdsfoot trefoil (*Lotus corniculatus* L.) grown for seed to varying levels of crop-water stress has not been described. The objectives of this study are to determine the effects of irrigation timing and amount on reproduction and seed yield for three crop years. Six treatments varying in water depletion percentage and replenishment amount were applied in 1994 and 1995 on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll) near Corvallis, OR. In 1996, only the low-stress (LS) and non-irrigated control (C) treatments were investigated. In the first year of production, maintaining plants under low-stress conditions sustained flowering longer than with limited or no irrigation applications. Flowering is not affected by irrigation in subsequent years of production. Total above-ground phytomass production is correlated with the amount of applied irrigation water (r = 0.92). In 1994, all single application irrigation treatments and the C treatment have greater harvested seed yields than the LS treatment. In 1995, all single irrigation treatments have greater harvested SY than the LS treatment. There are no difference between the LS and C in 1995 and 1996. Umbel density and number of seeds per pod are the primary determinants of total seed yield (r = 0.77 and 0.92, respectively). Optimal seed production is achieved by not irrigating this crop.

Introduction

Birdsfoot trefoil is a perennial, non-bloating forage legume used for pasture, hay and silage in the midwestern and northeastern USA and eastern Canada. Annual USA seed production is estimated to be about 83 t from 830 ha (AOSCA, 1994). Seed yields range from 50 to 560 kg ha^{-1} (Seaney and Henson, 1970; McGraw and Beuselinck, 1983; White et al., 1987; Li and Hill, 1989;) with 50 to 170 kg ha^{-1} considered as average (Seaney and Henson, 1970; McGraw and Beuselinck, 1983; Winch et al., 1985). Though the wide range in seed yield is in part due to shattering, soil-water availability may also be a factor that constrains birdsfoot trefoil seed yields. Research has been carried out on birdsfoot trefoil seed production and some of the most important limiting factors have been identified (Fairey, 1994). However, there is no information available on water management of birdsfoot trefoil grown for seed.

Water management practices for maximal seed production of forage legume seed crops are distinct from those for hay or pasture crops (Hutmacher et al., 1991; Steiner et al., 1992). In forage legume seed crops, different responses to both high and low soil-water availability are found. In most crops, appropriate soil-water availability is needed to promote flower development, pollination, seed growth and maturation. Water management strategies for forage legume seed production vary among species. Species have distinct responses for water stress adjustment and there is no general water management strategy for all forage legume seed crops. Alfalfa and white clover seed yields can be optimized by limiting the plant vegetative growth by controlled water stress (Clifford, 1985; 1986; Steiner et al., 1992, Oliva et al., 1994c). Red clover, however, responds optimally when there is no or low water stress during the reproductive phase of growth (Oliva et al., 1994b). Optimal irrigation management also can differ between the years when the crop is first established to that of successive years of seed production (Oliva et al., 1994a;

1994c) and by the quantity of stored water into the soil profile during the winter (Steiner et al., 1992).

The most important birdsfoot trefoil seed yield component is the number of umbels or inflorescens per unit area (Albretchsen et al., 1966; Bresciani and Frakes, 1973; Pankiw et al., 1977; McGraw et al., 1986a; Stephenson, 1984; Li and Hill, 1988; 1989). Management practices that reduce the number of umbels per unit of area will ultimately decrease seed yield. When the number of umbels are not limited, yield components such a number of florets per umbel, number of seeds per pod, number of pods per umbel, and seed weight may influence seed yield.

The objective of this research is to determine the effects of irrigation timing and amount on birdsfoot trefoil reproductive development, seed yield, and yield components.

Materials and Methods

The experiment was conducted in 1994, 1995, and 1996 at the Oregon State University, Hyslop Field Laboratory near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll). The experimental area was fumigated with methyl bromide (360 kg ha^{-1}) preceeding seedbed preparation to evenly control weeds. Birdsfoot trefoil 'MU-81' (Beuselinck and McGraw, 1986) was planted 30 August 1993 into a level seedbed in single rows 0.6 m apart and at a rate of 2.3 kg ha^{-1}. Water was applied with high-pressure overhead sprinklers just after planting and as needed the following 22 days to establish the crop. Common agronomic practices for forage legume seed production including weed and insect control were used (Chapter 3). Four honey bee (*Apis mellifera* L.) hives were placed close to the experimental area each year at the time of initial bloom.

The plots were arranged in a randomized complete block design with four replications and six treatments in 1994 and 1995. Two of the six treatments were used in 1996. Each plot was 4.5 m wide by 10 m long and was surrounded by a furrow with dikes to prevent lateral surface water movement if application rates exceeded the soil-water infiltration rate. The 1-m wide alleys at the ends of each plots were also diked.

A surface trickle irrigation system delivered water to each plot through 3.5 L h^{-1} in-line, turbulent-flow emitters spaced 0.9 m apart in five plastic drip lines 60 cm apart and perpendicular to the planting rows. A distribution manifold consisting of a mesh filter, ball valve, residential water flowmeter, volumetric controller, and a pressure regulator allow water to be applied to all four replications of each treatment at the same time.

For 1994 and 1995, five supplemental irrigations treatments were applied between the period from clip-back to seed harvest. The treatments were: (i) low-stress (LS), the soil-water content was maintained close to 100% field capacity (FC) by two or three water application replacements per week during the period from early-June until three weeks before seed harvest; (ii) single water replacement to 50% FC when soil-water depletion was 30% (D30-F50); (iii) single water replacement to 100% FC when soil-water depletion was 30% (D30-F100); (iv) single water replacement to 50% FC when soil-water depletion was 60% (D60-F50); (v) single water replacement to 100% FC when soil-water depletion was 60% (D60-F100); and (vi) a non-irrigated control (C). In 1996, only treatments LS and C were evaluated.

The soil-water status of each treatments was monitored weekly from the time of forage removal until harvest by neutron attenuation (Cuenca, 1988). The neutron attenuation measurements were calibrated using available published data for the same local conditions (Oliva, 1992). Readings were taken 48 h after each irrigation at depths of 0.45, 0.65, 0.95, 1.25, 1.55 and 2.00 m below the soil surface in all plots. Procedures for determining volumetric soil-water content, total available soil-water, and fraction of available water used (FAWU) are described in Chapter 3. Seasonal estimated crop evapotranspiration (ET_c) was the sum of applied water, precipitation, and the change in soil-water content estimated by neutron attenuation (Cuenca, 1988). Based on the neutron attenuation readings at the deepest soil depths measured, it was assumed that no deep percolation occurred in 1994 and 1995. Drainage through the soil profile was presumed to have occurred in 1996 through root channels of plants that died during the winter 1996 (Chapter 3).

To determine the plant water-stress status, five measurements were taken at least once a week in all plots from 24 June (DOY 175) to 25 August (DOY 237) in 1994; from 17 July (DOY 198) to 25 August (DOY 237) in 1995; and from 5 July (DOY 186) to 22 August (DOY 234) in 1996 on clear, cloud-free days, and between 1200 to 1400 h. Measurements were taken 1 m from the top of the canopy at a 45° oblique angle facing northwest from both sides of the longer west-east axis of each plots. To estimate the soil-induced plant-water stress, a crop water stress index (CWSI) was estimated (Idso et al.,1981a) using a Scheduler (Plant Stress Monitor, Carborondum Co. Solon, OH) to measure crop canopy temperature, air temperature, and water vapor pressure deficit (Chapter 3).

Flower and pod density were estimated weekly using six 0.1 m^2 random samples per plot from the time of first bud appearance until seed harvest. The pods were classified (Winch et al., 1985) as: (i) immature pods, pod color ranges from dark green to light green; (ii) mature pods, pod color is green-white to dark brown; and (iii) dehisced pods, pods begin to twist and dehisce and the seeds shatter. Peak flowering was defined as the time when the maximum flower density was initially obtained.

Seed loss due to shattering was determined every Monday, Wednesday, and Friday by collecting shattered seeds from two pans (60 x 40 x 10 cm) placed 10 cm above the soil surface between two planting rows and below the crop canopy of each plot. The shattered seeds were collected with a vaccum, cleaned, and weighed. Shattered seeds at harvest was calculated as the sum of all seeds collected from the time of initial seed shattering until harvest time.

Harvest time was decided to be when most pods were light-tan to brown-colored, the number of mature pods had reached a maximum, and shattering had begun. Two subplots 1 x 4 m were harvested from both ends of each plot by a gas-powered mower in the early-morning to avoid seed shatter losses. The plant materials were collected by hand, bagged, and dried at 32° C for 1 day. Above-ground phytomass was weighed, the seeds threshed from the plant material, and the seeds cleaned and weighed. Harvested seed yield (SY) is the amount of non-shattered seeds at harvest time. Total above-ground phytomass (TAGP) is above-ground phytomass minus harvested SY. Harvest index (HI) was calculated by dividing the SY by TAGP. Total SY is the sum of SY plus the accumulated shattered seed losses until harvest time. Seed yield components were estimated from mature umbels collected from six 0.1 m^2 random samples taken at harvest time. The number of pods per umbel were estimated from 20 random umbels per sample, number of seeds per pod from 40 random pods, and mean seed weight from four random samples of 200 seeds.

The effect of soil-water availability on the relative contribution of each seed yield components was determined by path-coefficient analysis (Oliva et al., 1994b, 1994d). This analysis quantifies the direct influence of one yield component upon another and allows the partitioning of the correlation coefficient into direct and indirect effects (Li, 1956; Dewey and Lu, 1959). The variables included in the path-coefficient analysis and the nature of their causal relationship are shown in Fig 4.1. Path-coefficient analysis has been previously used for determining seed yield component relationships among birdsfoot trefoil genotypes (Albrechtsen et al., 1966).

Regression analysis was performed to determine the relationships of total SY with FAWU at time of irrigation, seasonal ETc, and seasonal CWSI.

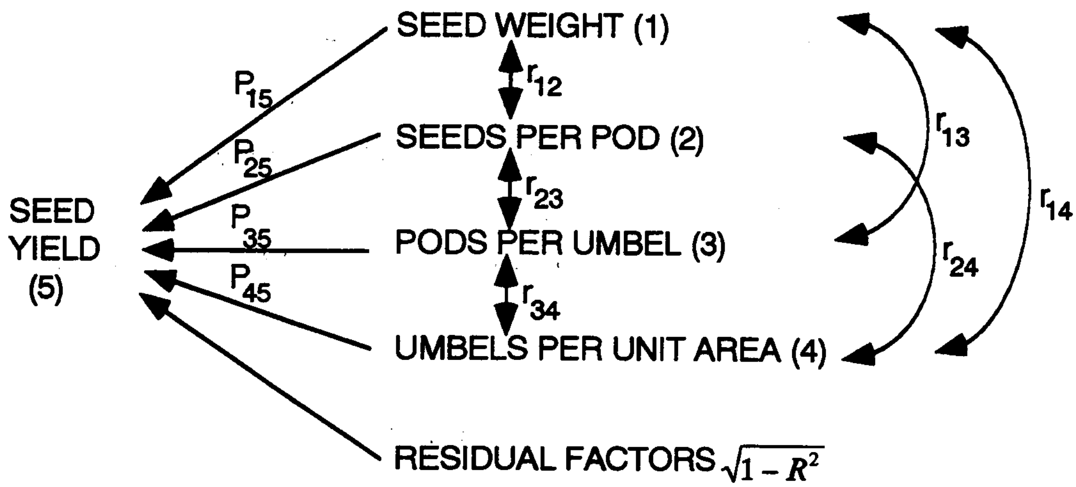

Fig. 4.1. Causal relationships of the path-coefficient analysis for birdsfoot trefoil seed production using six irrigation treatments. Doubled-arrowed lines indicate mutual associations that are measured by correlation coefficients (r_{ij}), and the single-arrowed lines represent direct influence as measured by path-coefficients (P_{ij}).

Regression analysis was also used to test the relationship between TAGP with seasonal ETc and seasonal CWSI. Standard errors of the mean were estimated for number of flowers and amount of shattered seeds. The nature of the associations of seed yield components with soil and crop-water status was determined by Pearson's correlation coefficients (Snedecor and Cochran, 1980). Analysis of variances were computed for all variables to test differences among irrigation treatments. Student's *t* pairwise comparison was used to contrast plant responses within treatments among years. Differences reported are significant at $P \leq 0.05$, unless otherwise is indicated.

Results and Discussion

Inflorescence development

The dates of irrigation initiation for LS treatment were similar all three years (June 8, DOY 160 for 1994 and 1995; and June 7, DOY 159 for 1996). The time of application of the single water replacements for the rest of the treatments were delayed in 1995 until soil-water depletion levels were similar to those of 1994. The soil-water content at the time of the irrigation initiation for LS treatment was different in the three years due to different amounts of precipitation received during the spring, prior to irrigation treatment applications. The amount of available soil-water that had been depleted at forage removal time was 16, 11, and 20% in 1994, 1995 and 1996, respectively. The amounts of precipitation received from March to May were 165, 290, and 315 mm, in 1994, 1995, and 1996, respectively (Apendix, Table 1).

The time of initial flowering was similar each year (DOYs 181, 180, and 183 in 1994, 1995 and 1996, respectively; Fig 4.2), indicating a strong photoperiodic response. In 1994, the duration of the flowering period increased

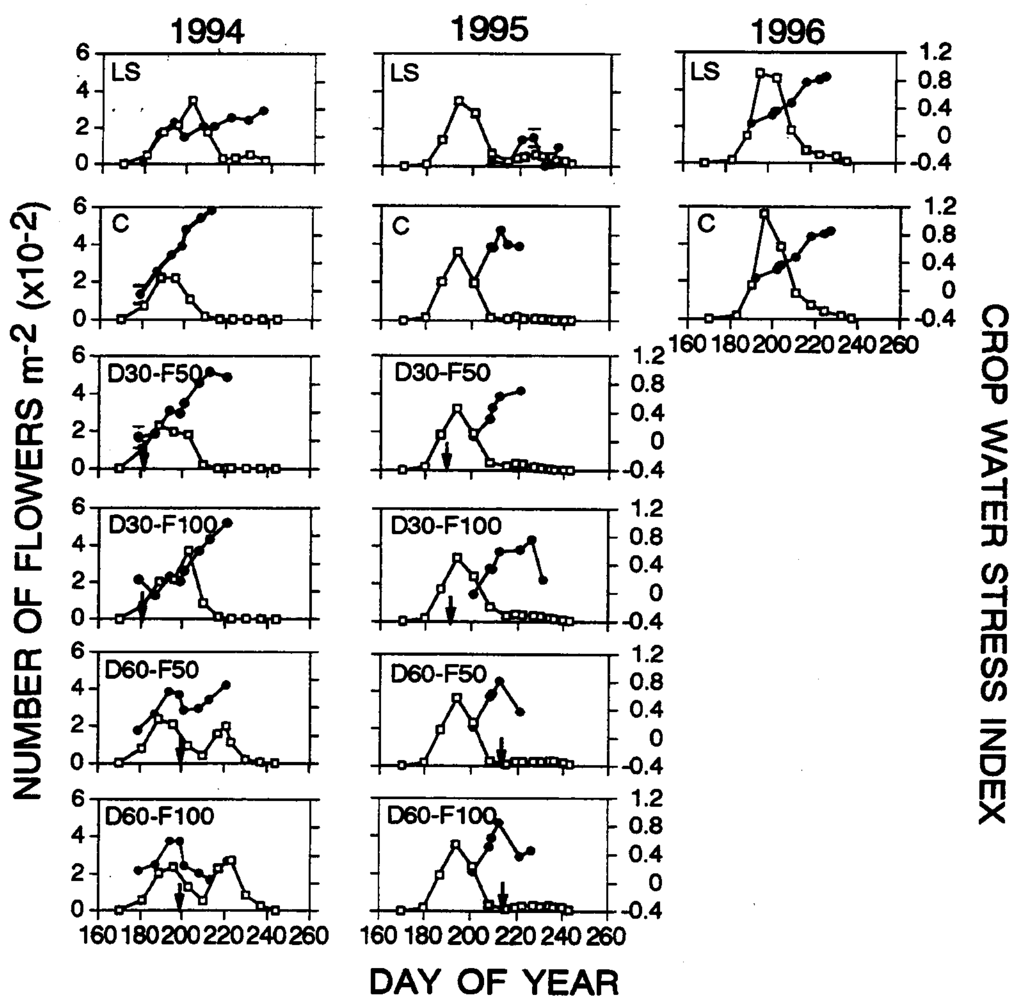

Fig. 4.2. Number of flowers (□) and crop water stress index (CWSI) (●) until harvest time for six birdsfoot trefoil irrigation treatments in 1994 and 1995, and two in 1996. Treatments are indicated on the upper-right corner of each graph. Arrows and vertical lines indicate time of irrigation application (not shown for LS treatment) and standard error of the mean, respectively.

as the soil-water availability increased. Because of lower levels of plant stress measured by CWSI, treatments LS and D30-F100 maintained longer flowering periods than treatments D30-F50 and C (Fig. 4.2). Treatments with limited applications or no irrigation before the time of peak flowering (D30-F50 and C) had shorter periods of flowering than higher application amount treatments. Peak flowering was reached at 8 July (DOY 189) for treatments D30-F50 and C, and on 22 July (DOY 223) for treatments LS and D30-F100.

A bimodal flowering pattern occurred in treatments D60-F50 and D60-F100. The first flowering peak occurred prior to water application and was the result of available stored soil-water remaining from spring precipitation. As soil-water was depleted, flower production declined in a manner similar to that of the unirrigation control (Fig. 4.2). With the delayed water application (DOY 199) after the initial flowering peak (DOY 189 to 196), flower production was reinitiated after the irrigation application. This did not occur in the 30% depletion treatments because the duration of flowering was extended when the application of water was before the decline in flowering.

In 1995 and 1996, there were no differences in the duration or time of peak flowering among any of the treatments (DOY 194 and 196, respectively; Fig. 4.2). Red clover grown for seed shows a similar first-year flowering response related to water treatments with no difference in time of peak flowering in the second-year (Oliva et al., 1994b). Water is depleted from greater depths in the second and third years of production during flowering and pod development stages of development (Chapter 3). As a result, more soil-water is available for a greater amount of time which is able to help sustain flowering longer in the second and third years of production.

Flowering occurs from continuous shoot succession with continued shoot replacement of older shoots as they die. New shoots become fertile under appropriate conditions for flower induction (Li and Hill, 1988). This may explain the lower seed yield efficiencies in 1995 compared to 1994, and 1996. In 1995, excepting D30-F100 treatment, the number of inflorescences decreased in the range from 17 to 52% (Chapter 4). Seed amount per pod and seed weight also decreased.

Total phytomass and seed yield

Harvested SY is the amount of seed produced by pods that have not shattered at harvest time. The amount of harvested SY was generally greater for all treatments in 1994 than in 1995 and 1996 (Table 4.1). This may have been due to the plants developing successively more extensive root systems with each year of production (Chapter 3) or to more soil-water available in 1995 and 1996 than in 1994. In 1994, all deficit irrigation treatments and the non-irrigated control had greater harvested SY than the LS treatment. In 1995, all single irrigation treatments had greater harvested SY than the LS treatment. There were no difference between the LS and non-irrigated control in 1995 and 1996.

In 1994 and 1995, there was a greater percentage of the total seed yield shattered in the LS than the rest of the irrigation treatments (exception: treatment D30-F50 in 1994). The period of pod development is greater for the LS than the rest of the treatments, so the amount of time for pods to shatter during the extended period of pod development is correspondingly longer. There are no seed shatter percentage differences between the LS and non-irrigated control in 1996.

Only in 1994 were there any differences among irrigation treatments for total seed yield production. Total seed yield is the sum of harvested seed yield and shattered seed production at the time of seed harvest. The non-irrigated control and 60% depletion irrigation treatments yielded the greatest amount of total seeds of all treatments. Total SY was related to soil-water status as a function of FAWU at time of irrigation (Fig 4.3). However, total SY was not related to CWSI (data not shown).

Table 4.1. Harvested, shattered, and total seed yield, shattered seeds relative to total seed yield, total above-ground phytomass (TAGP), and harvest index (HI) for six birdsfoot trefoil seed irrigation treatments in 1994 and 1995, and two treatments in 1996.

Treatment	Seed yield: Harvested	Seed yield: Shattered[†]	Seed yield: Total[‡]	Shattered seed to total seed yield	TAGP	Harvest Index[§]
	----------------------- Mg ha^{-1}	-----------------------	-----------------------	---- % ----	-- Mg ha^{-1} --	
Year 1994						
LS	0.19 c[¶]	0.128 b	0.32 c	37.3 a	9.5 a	2.0 c
D30-F50	0.52 b	0.204 a	0.73 ab	27.7 b	5.5 c	9.5 ab
D30-F100	0.54 b	0.083 bc	0.63 b	12.9 c	6.5 b	8.3 b
D60-F50	0.75 a	0.087 bc	0.84 a	10.5 c	5.9 bc	12.8 a
D60-F100	0.79 a	0.037 c	0.83 a	4.4 c	5.9 bc	13.5 a
C	0.69 a	0.077 b	0.76 a	10.0 c	5.0 c	13.6 a
Year 1995						
LS	0.13 b	0.053 ab	0.19 a	29.9 a	9.5 a	1.5 c
D30-F50	0.31 a	0.040 abc	0.35 a	11.5 b	5.8 cd	6.3 a
D30-F100	0.29 a	0.059 a	0.35 a	17.8 b	7.5 b	3.6 b
D60-F50	0.28 a	0.038 bc	0.32 a	12.7 b	6.0 cd	4.8 ab
D60-F100	0.32 a	0.038 bc	0.36 a	10.9 b	7.0 bc	4.7 ab
C	0.21 ab	0.022 c	0.23 a	11.0 b	4.9 d	4.3 b
Year 1996						
LS	0.19 a	0.051 a	0.24 a	21.7 a	8.6 a	2.2 b
C	0.26 a	0.093 a	0.35 a	17.3 a	5.0 b	5.1 a

Table 4.1. Continued.

Treatment	Seed yield			Shattered seed to total seed yield	TAGP	Harvest Index[§]
	Harvested	Shattered[†]	Total[‡]			
Seasonal contrast between years 1994 and 1995[#]						
LS	*	ns	ns	ns	ns	*
D30-F50	**	*	***	*	ns	**
D30-F100	*	ns	*	ns	ns	**
D60-F50	***	*	***	ns	ns	***
D60-F100	***	ns	***	*	*	***
C	***	ns	***	ns	ns	***

ns, *, **, *** Not significant, significant at 0.05, 0.01, and 0.001 probability levels, respectively.

[†] Accumulation of shattered seed until harvest date.

[‡] Sum of harvested seed plus shattered seed.

[§] Estimated as the ratio of harvested seed yield with total above-ground phytomass x 100.

[¶] Means within columns and years followed by a different letter are significantly different according to Fisher's protected LSD test at $P \leq 0.05$.

[#] Probability of that means of two years are different (Student's t-pairwise comparison).

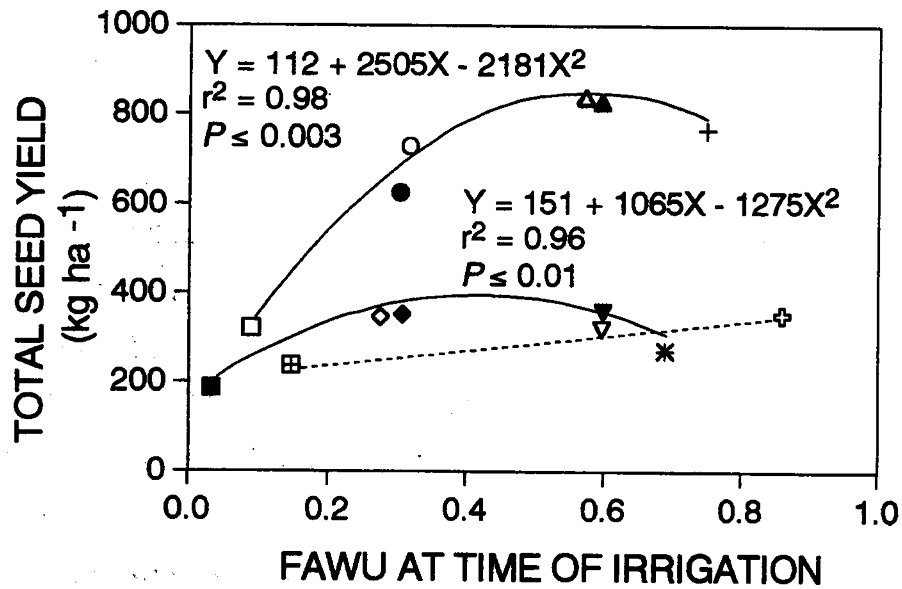

Fig: 4.3. Total seed yield (harvested plus shattered seeds) as a function of fraction of available water used (FAWU) at time of irrigation for six birdsfoot trefoil irrigation treatments in 1994, 1995, and two treatments in 1996. Symbols indicate: LS (□, ■, ⊞) and C (+, ✳, ✙) for 1994, 1995 and 1996, respectively. Symbols indicate: D30-F(50, 100) (○, ●), and (◇, ◆); and D60-F(50, 100) (△, ▲) and (▽, ▼) for 1994 and 1995, respectively.

In all years, plants receiving supplemental water applications produced more total above-ground phytomass (TAGP) that the non-irrigated control (Table 4.1). The amount of TAGP was correlated with the amount of applied irrigation water (Table 4.2). The amount of TAGP produced was also related to those variable that indicate low plant water-stress (e.g., high ET_c, Fig. 4.4 and low CWSI, Fig. 4.5). The efficient conversion of water to TAGP suggests that no luxury water consumption occurs (Chapter 3). Based on the slope of the regression equation (total ET_c dependent on applied water), 45% of the water applied results in direct water use increases (Fig. 4.6). This compares to values of 52.0, 62.2, and 64.2% for alfalfa, white clover, and red clover grown for seed, respectively (Hutmacher et al., 1991, Oliva et al., 1994c, and Oliva et al., 1994a). These data suggest that birdsfoot trefoil is not as an efficient utilizer of supplemental irrigation water as the three other forage legume seed crops.

The LS treatment had the lowest harvest Index (HI) of all treatments in all three years (Table 4.1). The HI is correlated with seed yield water use efficiency ($r = 0.78$; $P \leq 0.001$) indicating that plant growth conditions that most efficiently produce seed also result in the greatest reproductive efficiency (Chapter 3). As vegetative growth increases in relationship to reproductive development, the resulting competition delays flower development (Li and Hill, 1988). Similar findings are reported in white clover in a second seed year of production in which seed yield was substantially lower because of dense stolon production at the expense of inflorescence development (Oliva et al., 1994d).

Seed yield components

The different water management treatments affected the combinations of significant seed yield components differently both years (Table 4.2). In 1994, total SY variation was positively associated with the direct effects of number of

Table 4.2. Relationships among birdsfoot trefoil seed yield and seed shattering with soil and water variables.

Variable	Variable				
	Harvested seed yield	Total seed yield	Percentage shattered seed	TAGP	Harvest index
Average ET_c	-.406	-.340	.668**	.021	-.498
Total ET_c	-.304	-.228	.746**	.874***	-.425
Crop coefficient (k_c)	-.224	-.149	.666**	.761**	-.336
CWSI	.351	.325	-.601*	-.899***	.474
FAWU	.347	.351	-.483	-.883***	.455
Soil-water change	.297	.339	-.239	-.717**	.406
Precipitation	-.455	-.515	.046	.268	-.453
Applied water	-.291	-.270	.549*	.900***	-.428

The symbols *, **, and *** indicate significance at $P \leq 0.05$, 0.01, and 0.001, respectively.

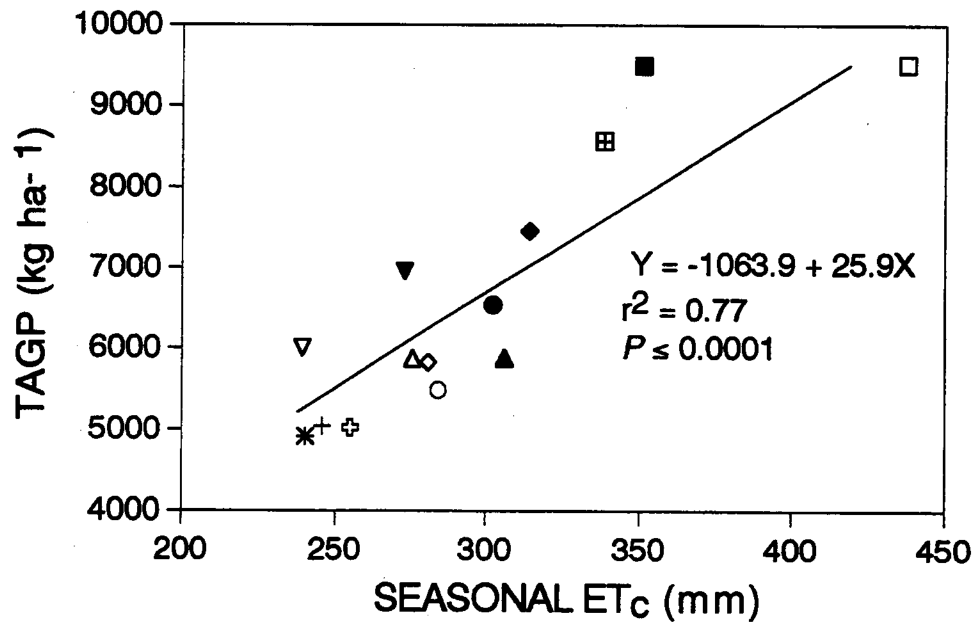

Fig. 4.4. Total above-ground phytomass (TAGP) as a function of average estimated crop evapotranspiration (ET_c) for six birdsfoot trefoil irrigation treatments in 1994 and 1995, and two treatments in 1996. Symbols indicate: LS (□, ■, ⊞) and C (+, ✳, ✙) for 1994, 1995 and 1996, respectively. Symbols indicate: D30-F(50, 100) (○, ●), and (◇, ◆); and D60-F(50, 100) (△, ▲) and (▽, ▼) for 1994 and 1995, respectively.

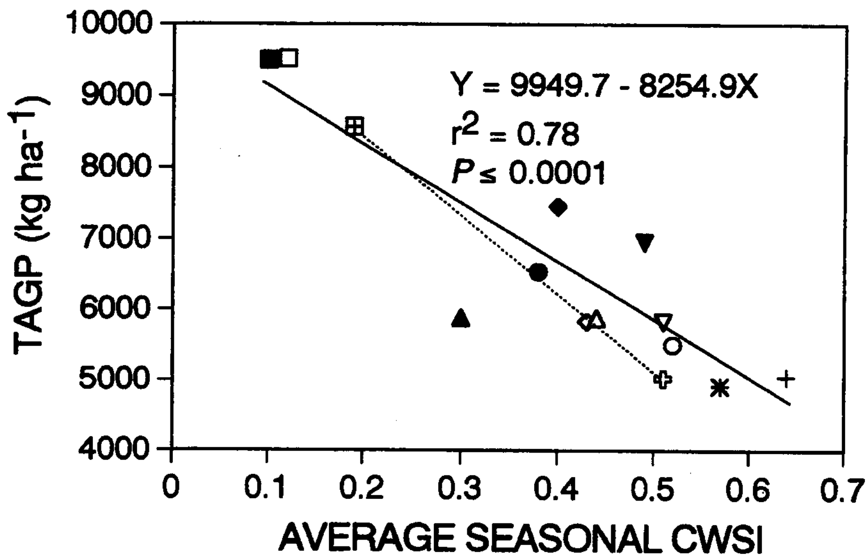

Fig. 4.5. Total above-ground phytomass (TAGP) as a function of average seasonal crop water stress index (CWSI) for six birdsfoot trefoil irrigation treatments in 1994, 1995, and two treatments in 1996. Symbols indicate: LS (□, ■, ⊞) and C (+, ✳, ✙) for 1994, 1995 and 1996, respectively. Symbols indicate: D30-F(50, 100) (○, ●), and (◇, ◆); and D60-F(50, 100) (△, ▲) and (▽, ▼) for 1994 and 1995, respectively.

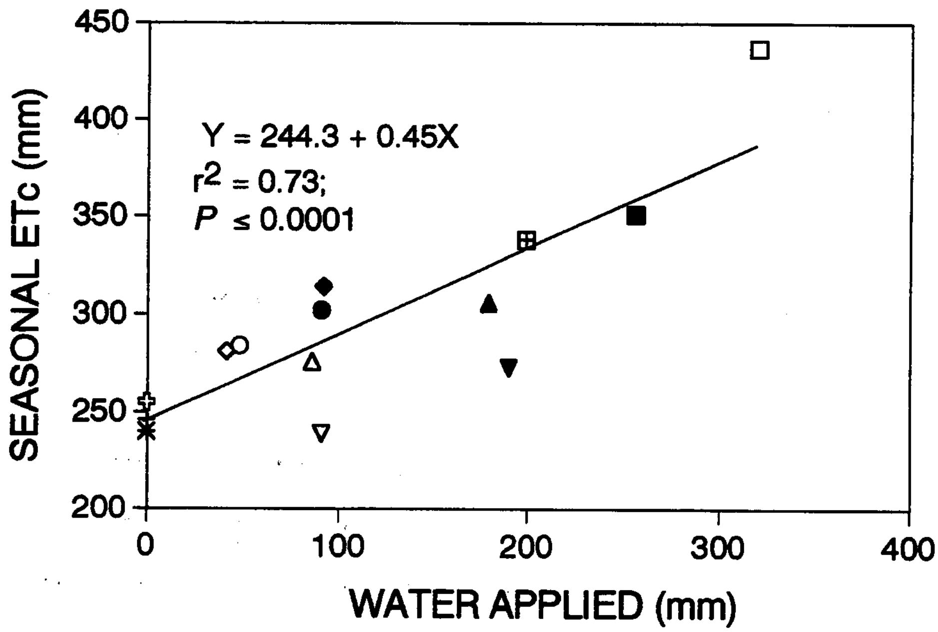

Fig. 4.6. Relationship of seasonal estimated crop evapotranspiration (ET_c) and amount of water applied for six birdsfoot trefoil irrigation treatments in 1994 and 1995. Symbols indicate: LS (□, ■, ⊞) and C (+, ✳, ✣) for 1994, 1995 and 1996, respectively. Symbols indicate: D30-F(50, 100) (○,●), and (◇, ◆); and D60-F(50, 100) (△, ▲) and (▽, ▼) for 1994 and 1995, respectively.

umbels produced (umbel density) and seeds per pod (Table 4.3). Delaying water application (60% depletion treatments) and applying the lower amount of water (50% replacement) resulted in the greatest umbel density. The LS treatment extended the period of flowering, but this decreased the umbel density and number of seeds per pod. The rest of seed yield components were unaffected by the irrigation treatments.

In 1995, total SY was negatively associated with the direct effect of pods per umbel (Table 4.4). The LS treatment had the lowest umbel density, number of seeds per pod, and seed weight of all treatments (Table 4.3). With the most delayed water application time and the greatest water replenishment amount (D60-F100), umbel density and seed weight were optimized. The lower water replenishment amount (D60-F50) resulted in the greatest number of seeds produced per pod at the expense of umbel density, with no effect on total SY (Table 4.1). In 1996, the number of pods per umbel was greater in the LS than non-irrigated control. Except for the number of pods per umbel, the rest of seed yield components were unaffected by the irrigation treatments. Maintaining the plants under low water stress conditions reduced the number of seeds produced per pod all three years.

The umbel density ($r = 0.77$; $P \leq 0.001$) and number of seeds per pod ($r = 0.92$; $P \leq 0.001$) are the primary determinants of total seed yield. Umbel density has been previously cited as the most significant seed yield component (Albretchsen et al., 1966; Bresciani and Frakes, 1973; Pankiw et al., 1977; McGraw et al., 1986a; Stephenson, 1984; Li and Hill, 1988; 1989), but the significance of the number of seeds per pod has not been previously reported in other agronomic studies. The previously published reports focused primarily on yield component differences during different growing season times rather than differences among treatments imposed within the same growing season.

With conditions that increase ET_c (Chapter 3), umbel density is decreased ($r = -0.53$; $P \leq 0.05$) and the number of pods per umbel increased. However, the number of pods per umbel is negatively associated with seed

Table 4.3. Effect of six irrigation treatments in 1994 and 1995, and two treatments in 1996 on birdsfoot trefoil seed yield components.

	Yield components			
Treatment	Umbels	Pods	Seeds	Seed weight
	no. m^{-2}	no. $umbel^{-1}$	no. pod^{-1}	mg $seed^{-1}$
Year 1994				
LS	846 d†	3.6 a	11 b	1.25 a
D30-F50	1555 c	3.6 a	22 a	1.26 a
D30-F100	1118 d	3.2 a	20 a	1.19 a
D60-F50	2639 a	3.5 a	21 a	1.24 a
D60-F100	1474 c	3.6 a	20 a	1.22 a
C	1995 b	3.4 a	18 a	1.24 a
Year 1995				
LS	699 d	4.0 a	8 c	0.91 d
D30-F50	901 cd	4.0 a	10 b	1.13 b
D30-F100	1322 b	4.3 a	11 b	1.05 c
D60-F50	1259 b	4.6 a	15 a	1.17 ab
D60-F100	1590 a	4.3 a	9 bc	1.20 a
C	1002 c	4.3 a	11 b	1.11 bc
Year 1996				
LS	1058 a	4.8 a	9 a	0.96 a
C	1009 a	4.1 b	13 a	1.03 a

† Means within columns and years followed by a different letter are significantly different according to Fisher's protected LSD test at $P \leq 0.05$.

Table 4.4. Path-coefficient analyses of birdsfoot trefoil seed yield components across six irrigation treatments in 1994 and 1995.

Pathway	1994	1995
Seed weight *vs.* total seed yield:		
Direct effect, P_{15}	-0.02 ns	0.25 ns
Indirect effects[†]:		
via seeds per pod, $r_{12}P_{25}$	-0.06	0.14
via pods per umbel, $r_{13}P_{35}$	0.00	-0.04
via umbels per unit area, $r_{14}P_{45}$	0.05	0.16
Correlation, r_{15}	-0.03 ns[‡]	0.51**
Seeds per pod *vs.* total seed yield:		
Direct effect, P_{25}	0.56**	0.28 ns
Indirect effects:		
via seed weight, $r_{12}P_{15}$	0.00	0.13
via pods per umbel, $r_{23}P_{35}$	-0.01	-0.10
via umbels per unit area, $r_{24}P_{45}$	0.21	0.06
Correlation, r_{25}	0.76**	0.37**
Pods per umbel *vs.* total seed yield:		
Direct effect, P_{35}	0.09 ns	-0.35*
Indirect effects:		
via seed weight, $r_{13}P_{15}$	0.00	0.03
via seeds per pod, $r_{23}P_{25}$	-0.04	0.08
via umbels per unit area, $r_{34}P_{45}$	0.00	0.13
Correlation, r_{35}	0.05 ns	-0.11 ns
Umbels per unit area *vs.* total seed yield:		
Direct effect, P_{45}	0.37*	0.31 ns
Indirect effects:		
via seed weight, $r_{14}P_{15}$	0.00	0.13
via seeds per pod, $r_{24}P_{25}$	0.31	0.05
via pods per umbel, $r_{34}P_{35}$	0.00	-0.14
Correlation, r_{45}	0.68**	0.35**

ns, *, ** Not significant and significant at the 0.05 and 0.01 probability levels.

† Indirect effects are the partitioning of the correlation coefficient that are due to colinearity effects of the remaining seed yield components. There is not test of significance for indirect effects.

‡ The correlation coefficient is the sum of the direct and indirect effects.

yield (r = -0.75; $P \leq 0.01$). This suggests that conditions that are conducive to increasing the number of pods per umbel are not advantageous for increasing the number of seeds produced within each pod. It may be that birdsfoot trefoil pods are not able to support all fertilized ovules through seed maturity beyond a threshold of seed set. This has been suggested as a mechanism that limits the number of seeds produced per pod in red clover (Clifford and Scott, 1989). The number of seeds per pod has been shown to be a significant determinant of seed yield differences among birdsfoot trefoil genotypes (Bresciani and Frakes, 1973).

Conclusions

The effect of plant water status on birdsfoot trefoil reproductive development, seed yield, and seed yield components is dependent on the year of seed production and amount of plant-water stress affected by irrigation timing and amount of application. In the first year of seed production, maintaining plants under low-stress conditions sustain flowering longer than with limited or no irrigation applications. Treatments with limited applications or no irrigation before the time of peak flowering have shorter periods of flowering than higher application amount treatments. A bimodal flowering pattern occurs when flower production declines as available stored soil-water from spring precipitation is depleted but then replenished which reinitiates flowering. Flowering is not affected by irrigation in the two subsequent years of seed production. Total above-ground phytomass production is strictly correlated with the amount of applied irrigation water. The harvest index is correlated with seed yield water use efficiency, indicating that plant growth conditions that most efficiently produce seed also result in the greatest reproductive efficiency.

In 1994, all single application irrigation treatments and the non-irrigated control have greater harvested seed yields than the LS treatment. In 1995, all single irrigation treatments have greater harvested SY than the LS treatment.

There are no difference in total seed yield between the LS and C in 1995 and 1996. Umbel density and number of seeds per pod are the primary determinants of total seed yield. Pods per umbel is also significant, but depended on the year of seed production. In 1994 and 1995, there is greater percentage of total seed yield shattered in the LS treatment (39 and 30%, respectively) than the rest of the irrigation treatments. The period of pod development is greater for the LS than the rest of the treatments, so the amount of time for pods to shatter during the extended period of pod development is correspondingly longer. There are no differences in the seed shatter percentage between the LS and non-irrigated control in 1996. Optimal seed production is achieved in western Oregon by not irrigating this crop.

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CHAPTER 5

BIRDSFOOT TREFOIL SEED PRODUCTION: III. SEED SHATTER AND OPTIMAL HARVEST TIME

Abstract

Seed shattering is a major problem in birdsfoot trefoil (*Lotus corniculatus* L.) seed production and limited information is available describing the effects of agronomic practices on seed shatter losses. The objectives of this research are to: (i) quantify the effects of soil-water availability on birdsfoot trefoil seed shatter and (ii) determine optimal harvest time based on a heat unit method to minimize seed losses due to shattering. Six treatments varying in water depletion percentage and replenishment amount were applied in 1994 and 1995 on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll) near Corvallis, OR. In 1996, only the low-stress (LS) and non-irrigated control (C) treatments were investigated. The total amount of shattered seeds is correlated with total harvested seed yield (r = 0.96). Manipulation of the reproductive development pattern by different water application times and amounts does not affect the time of peak seed shattering events. Crop-water stress status affects the percentage of total shattered seeds shattered at harvest time (r = -0.76). Increasing amounts of applied water increase the percentage of potential shatter losses that will shatter by harvest time (r = 0.65). Seed shatter losses fluctuate during the reproductive development period but are not influenced by the water application treatments. Fluctuations are also observed for the climatic variables average temperature, relative humidity, and vapor pressure deficit, but these cannot be used to predict the time of peak seed shatter events. A total of 109 HU are needed from the time from initial pod dehiscence until rapid

shattering occurs. The average seed yield loss per day due to shattering from pod dehiscence is 3 to 5.3 kg ha^{-1}.

Introduction

Birdsfoot trefoil (*Lotus corniculatus* L.) is a perennial, non-bloating forage legume used for forage and hay production in the northeastern and midwestern USA and eastern Canada. Research has been carried out on birdsfoot trefoil seed production and some of the most important factors limiting yield have been identified (Fairey, 1994). Seed shattering is a major problem in birdsfoot trefoil seed production (Seaney and Henson, 1970; Li and Hill; 1989). The anatomical configuration of tissues in the birdsfoot trefoil pods is related to the dehiscence mechanism. Dehiscences occurs along the ventral and dorsal sutures of the carpel margins and along the median vein of the pod (Esau, 1960). Pod dehiscence is caused by different rates of moisture loss in these tissues.

As plant maturity advances, the potential for seed yield potential increases because the total number of pods that are produced and mature on this indeterminate plant increases. As later developing pods mature, the percentage of pods that dehisce and seeds shattering increase (MacDonald, 1946; Anderson, 1955). The anatomy, development, and maturation of birdsfoot trefoil pods has been extensively studied. The physical factors that trigger pod dehiscence and seed shattering are well understood, but the effects after pod maturation are not well defined as well as the effects of agronomic practices such as water management on seed shattering.

Stages of pod development have been described based on changes in pod color. The pod color can vary from dark-green or dark-green-purple to green-white and then to golden-brown (MacDonald, 1946; Anderson, 1955; Winch and MacDonald, 1961). Three physiological stages of pod and seed development have been characterized (Winch and MacDonald,1961): (i) pod elongation, where there is an increase in pod length, seeds are immature, pod color is dark-green, and there is a high seed moisture content; (ii) seed development, seed size, pod diameter, and rate of germination increase, pod pods become light-green in color, and no dehiscence has occurred; (iii) seed maturation, maximal germination percentage is reached, pod color changes to golden-brown, the pod moisture content decreases from 65 to 25%, and seed shattering is initiated. Maximal seed yield is obtained during the seed maturation stage.

Relative humidity is considered the most critical factor influencing pod dehiscence and seed shattering (Anderson, 1955; Metcalfe et al., 1957). Mature pods shatter freely when relative humidity is below of 40% (Anderson, 1955). At low temperatures and high relative humidity, the rate of shattering is less than at high temperatures and lower relative humidity (Metcalfe et al., 1957; McGraw and Beuselinck, 1983). Pod moisture content is influenced by ambient relative humidity which is a critical factor that determines when pods will dehiscence. The critical pod moisture percentage for shattering is between 10.05 and 10.39% (Metcalfe et al., 1957). Under sunny conditions, pod temperature can be 5° C higher than the ambient air temperature, resulting in a change in the relative humidity at the surface of the pod (Metcalfe et al., 1957). The moisture equilibrium between pods and the atmosphere is the primary factor responsible for pod dehiscence at a given relative humidity. Gershon (1961) found no correlation between relative humidity and pod dehiscence in plants grown under greenhouse conditions, but found these factors correlated with pod dehiscence when birdsfoot trefoil is grown under field conditions. This is likely due to humidity differences between these two kinds of environments (Grant, 1996).

The rate of shattering increases as the rate of water loss from the pods increases, but pods do not shatter as readily when pod drying proceeds slowly (Buckovic, 1952). Although dependent upon environmental conditions, when desiccants and plant growth regulators are used to manage vegetative growth, seed shattering can be reduced and seed yield increased (Wiggans et al., 1956). These findings suggest that factors other than relative humidity and pod moisture content alone may modify the pod shattering response. Summations of average daily temperatures have been used to explain when pod dehiscence and shattering will occur (Gataric et al., 1990).

Grant (1996) suggests that harvest timing is only partially effective for reducing seed losses from shattering because of the indeterminate flowering nature of birdsfoot trefoil. Estimates for proper harvest time has been based on the rate of appearance of the pods and pod color (Anderson, 1955, Winch and MacDonald, 1961; Hare and Lucas, 1984; Winch et al., 1985; Pieroni and Laverack, 1994) and the rate of development of reproductive structures (Li and Hill, 1989). Optimal harvest time is suggested to be when 70-78% of the pods picked at random throughout the field are mature (Winch et al., 1985). A delay in the seed harvest to allow the latest developing umbels to mature can result in a 50% decrease in seed yields (Winch and MacDonald, 1961). If harvest is delayed nine days from the time of maximal mature pod percentage, seed losses are as high as 67% (Anderson, 1955).

The objectives of this research are to: (i) quantify the effects of soil-water availability on birdsfoot trefoil seed shatter and (ii) determine optimal harvest time based on a heat unit method to minimize seed losses due to shattering.

Materials and Methods

The experiment was conducted in 1994, 1995, and 1996 at the Oregon State University Crop Science Hyslop Field Laboratory near Corvallis, OR on a Woodburn silt loam soil (fine-silty, mixed, mesic Aquultic Argixeroll). Details of the agronomic practices used to grow the crop are presented in Chapters 3 and 4. The plots were arranged in a randomized complete block design with four replications and six treatments in 1994 and 1995. Two of the six treatments were used in 1996 with each plot being 4.5 m wide by 10 m long. A surface trickle irrigation system delivered water to each plot through 3.5 L h^{-1} in-line, turbulent-flow emitters spaced 0.9 m apart in five plastic drip lines 60 cm apart and perpendicular to the planting rows. A distribution manifold consisting of a mesh filter, ball valve, residential water flowmeter, volumetric controller, and a pressure regulator allow water to be applied to all four replications of each treatment at the same time. The soil-water status of each plot was monitored weekly until harvest by neutron attenuation (Cuenca, 1988) to determine when to apply the irrigation treatments.

For 1994 and 1995, five supplemental irrigations treatments were applied between the period from clip-back to seed harvest. The treatments were: (i) low-stress (LS), the soil-water content was maintained close to 100% field capacity (FC) by two or to three water application replacements per week during the period from early-June until three weeks before seed harvest; (ii) single water replacement to 50% FC when soil-water depletion was 30% (D30-F50); (iii) single water replacement to 100% FC when soil-water depletion was 30% (D30-F100); (iv) single water replacement to 50% FC when soil-water depletion was 60% (D60-F50); (v) single water replacement to 100% FC when soil-water depletion was 60% (D60-F100); and (vi) a non-irrigated control (C). In 1996, only treatments LS and C were evaluated.

Flower and pod density were estimated weekly using six 0.1 m^2 random samples per plot from the time of first bud appearance until the end of the season. The pods were classified (Winch et al., 1985) as: (i) immature pods, pod color ranges from dark green to light green; (ii) mature pods, pod color is green-white to dark brown; and (iii) dehisced pods, pods begin to twist and dehisce and the seeds shatter. Peak flowering was defined as the time when the maximum flower density was initially obtained.

Seed loss due to shattering was determined every Monday, Wednesday, and Friday by collecting shattered seeds from two pans (60 x 40 x 10 cm) that were placed 10 cm above the soil surface between two planting rows and below the crop canopy of each plot. Elevation of the pans allowed air to circulate within the canopy and avoided condensation under the pan. The shattered seeds were collected with a vacuum, cleaned, and weighed. Shattered seed loss at harvest (SS_h) is the sum of shattered seeds collected from the time of initial shatter to the time of seed harvest. Total shattered seeds (SS_t) is the sum of all seeds collected to the end of the season. The percentage of total seed shatter loss at harvest ($SS_{\%\ h}$) is calculated by dividing SS_h by SS_t.

Harvest time was determined to be when most pods were light-tan to brown-colored, the mature non-dehisced pod density had reached a maximum, and seed shattering had been initiated (Chapter 3). At this stage of development, maximal harvested seed yield was obtained. Two subplots 1 x 4 m were harvested from both ends of each plot. Details of the harvest method are described in Chapters 3 and 4. Harvested seed yield is the amount of non-shattered seeds at harvest time. Total seed yield is the sum of the harvested seed yield plus the sum of shattered seed losses to harvest time (Chapters 3 and 4).

In preliminary examinations of different kinds of climatic data and based on the literature (Anderson, 1955; Metcalfe et al., 1957; McGraw and Beuselinck, 1983), average daily temperature (T), relative humidity (RH), and vapor pressure deficit (VPD) were chosen as variables to investigate as predictors of pod dehiscence and seed shattering. Daily high and low temperature (T_h and T_l, respectively) and relative humidity (RH) were obtained from an automated meteorological station located 400 m from the trial site. The vapor pressure deficit (VPD) was based on the UN-FAO modified Penman method as used in the calculations for the reference evapotranspiration (ET_r) (Cuenca, 1989). Appreciable errors may result when using different empirical methods when the wind is calibrated in the reference evapotranspiration (ET_r) values (Cuenca and Nicholson, 1982). The equation for VPD (mb) is:

$$VPD = (E_s - E_a) \quad [1]$$

where E_s = saturation of water pressure (mb); and E_a = actual water pressure (mb), and:

$$E_s = 33.8639\,[(0.0007\,T_{mean} + 0.8072)^8 - 0.000019\,\{1.8\,T_{mean} + 48\} + 0.001316] \quad [2]$$

where T_{mean} (°C) is determined on a daily basis, and:

$$T_{mean} = (T_h + T_l)\,2^{-1} \quad [3]$$

and:

$$E_a = E_s(RH\ 100^{-1}) \quad [4]$$

where RH = daily relative humidity (%).

Daily degree day heat units (HU) were calculated using Equation 4 minus a base temperature of 10° C, and:

$$HU = [(T_h + T_l)\,2^{-1}] - 10 \quad [5]$$

The number of accumulated heat units from the time of peak flowering to initial pod dehiscence (HU_{SSi}) in 1994 and 1995 is determined by the equation:

$$HU_{SSi} = -97.1 + 0.41HU \quad [6]$$

$$r^2 = 0.84;\ P \leq 0.01$$

based on the data collected in 1996.

To determine whether the estimation of seed harvest time based on accumulated heat units could be improved, a modification of equation 5 comprised of two function components was tested: (i) accumulation of HU (Equation 5) from the time of peak flowering to the time of initial seed shatter (first pods shatter) plus (ii) the accumulation of HU modified by a VPD threshold from the time of initial seed shatter to harvest time:

$$HU_{ac}h = \sum_{pf=1}^{sln} HUpf + \sum_{pf=sln+j}^{h} HUh \quad [7]$$

where $HU_{ac}h$ = accumulated heat units until harvest time (h), HU_{pf} = sum of heat units from the time of peak flowering (pf) to the time of initial seed shatter (s_{In}), and HU_h = sum of heat units from the time of initial seed shatter to the time of seed harvest (h). The efficacy of VPD threshold values to modify the accumulated heat unit model was determined with accumulated heat units with threshold values less than: 4.0, 4.0, 4.5, 5.0, 5.5, 6.0, and 6.5 mb. Few or no days with VPD values below 4.0 were observed during the reproductive period in the three years of the study. The VPD was selected as the threshold indicator based on theory that under conditions of high T and high RH (low VPD), pod dehiscence does not progress.

Analysis of variance was used to determine differences among irrigation treatments for amount of total shattered seeds. Pearson's correlation analysis (r) is used to test functional relationship between shattered seed losses with plant water stress index (CWSI) and soil-water status (fraction of available water used, FAWU) (Chapter 3). Differences between Pearson's r and Spearman's rank correlation coefficient (r_s) are used to determine whether functional relationships between variables and the rank orders among irrigation treatments are similar. Student's *t* pairwise comparison were used to contrast total shattered seed by irrigation treatments among the three years. Differences reported are significant at $P \leq 0.05$, unless otherwise is indicated.

Results and Discussion

Seed Shattering and Crop Water Management

Effect of water management on shattering

The total amount of shattered seeds (SS_h) is influenced by irrigation treatment (Table 5.1) and was correlated with total harvested seed yield (SY_h) ($r = 0.96$, $P \leq 0.001$). However, the relative rankings of the irrigation treatments by total harvested seed yield and total amount of shattered seeds (SS_t) differed ($r_s = 0.85$; $P \leq 0.001$). This suggests that manipulation of the reproductive

Table 5.1. Total accumulated and percentage of total shattered birdsfoot trefoil seeds that are lost by the time of seed harvest for six birdsfoot trefoil seed irrigation treatments in 1994 and 1995, and two treatments in 1996.

Treatment	Total shattered seed	Shattered seed lost at harvest time
	---------- kg ha^{-1} ----------	--------------- % ------------
Year 1994		
LS	184 c†	69.6 a
D30-F50	512 a	39.9 b
D30-F100	335 b	24.8 bc
D60-F50	499 a	17.4 bc
D60-F100	476 a	7.8 c
C	467 ab	16.6 b
Year 1995		
LS	68 c	79.3 a
D30-F50	252 a	16.0 c
D30-F100	192 ab	31.0 b
D60-F50	206 ab	18.5 c
D60-F100	150 bc	25.3 bc
C	154 bc	14.2 c
Year 1996		
LS	54 b	95.5 a
C	280 a	33.1 b

ns, *, **, *** Not significant, significant at 0.05, 0.01, and 0.001 probability levels, respectively

† Means within columns and years followed by a different letter are significantly different according to Fisher's protected LSD test at $P \leq 0.05$.

development pattern by water application timing and application amount has a significant effect on SY_h (Chapter 4) but crop-water stress status affects the SS_t. The SS_t is poorly correlated with CWSI and FAWU (r = 0.46; $P \leq 0.10$ and r = 0.51; $P \leq 0.06$, respectively. Total harvested seed yield is not correlated with CWSI and FAWU (r = 0.33; $P \leq 0.26$ and r = 0.35; $P \leq 0.22$, respectively).

The percentage of total seed shatter losses that are lost by the time of harvest ($SS_{\%\ h}$) is negatively correlated with CWSI and FAWU (r = -0.76; $P \leq$ 0.002 and -0.61; $P \leq 0.02$, respectively). As the amount of applied irrigation water increases, the $SS_{\%\ h}$ can be expected to increase (r = 0.65; $P \leq 0.01$) which increases seed yield losses by the time of harvest. There is no relationship between SS_h and $SS_{\%\ h}$ (r = 0.22; $P \leq 0.46$) which indicates that seed yield losses at harvest time are independent of potential seed shatter losses and can be managed separately from the resulting effects of cultural practices, such as irrigation management, on seed yield.

Season-long distribution of shattering

The amount of $SS_{\%\ h}$ per sampling period fluctuates during the reproductive development period (Fig. 5.1). The time of peak $SS_{\%\ h}$ fluctuations generally coincide among the different irrigation treatments. In 1994, peaks occurred on DOY 220, 229, and 238 but the amplitude of the fluctuations vary by water application amount. Plants grown under higher water stress conditions within treatment combination pairs (D30-F50, D60-F50, and C) started to shatter two to four days earlier and reached peak shatter time earlier than their lower water-stress compliment (D30-F100, D60-F100, and LS, respectively) (Fig. 5.1). In 1995 and 1996, the $SS_{\%\ h}$ peaks occurred on DOY 226, 233, and 240 and DOY 228 and 235, respectively. Shattering time is

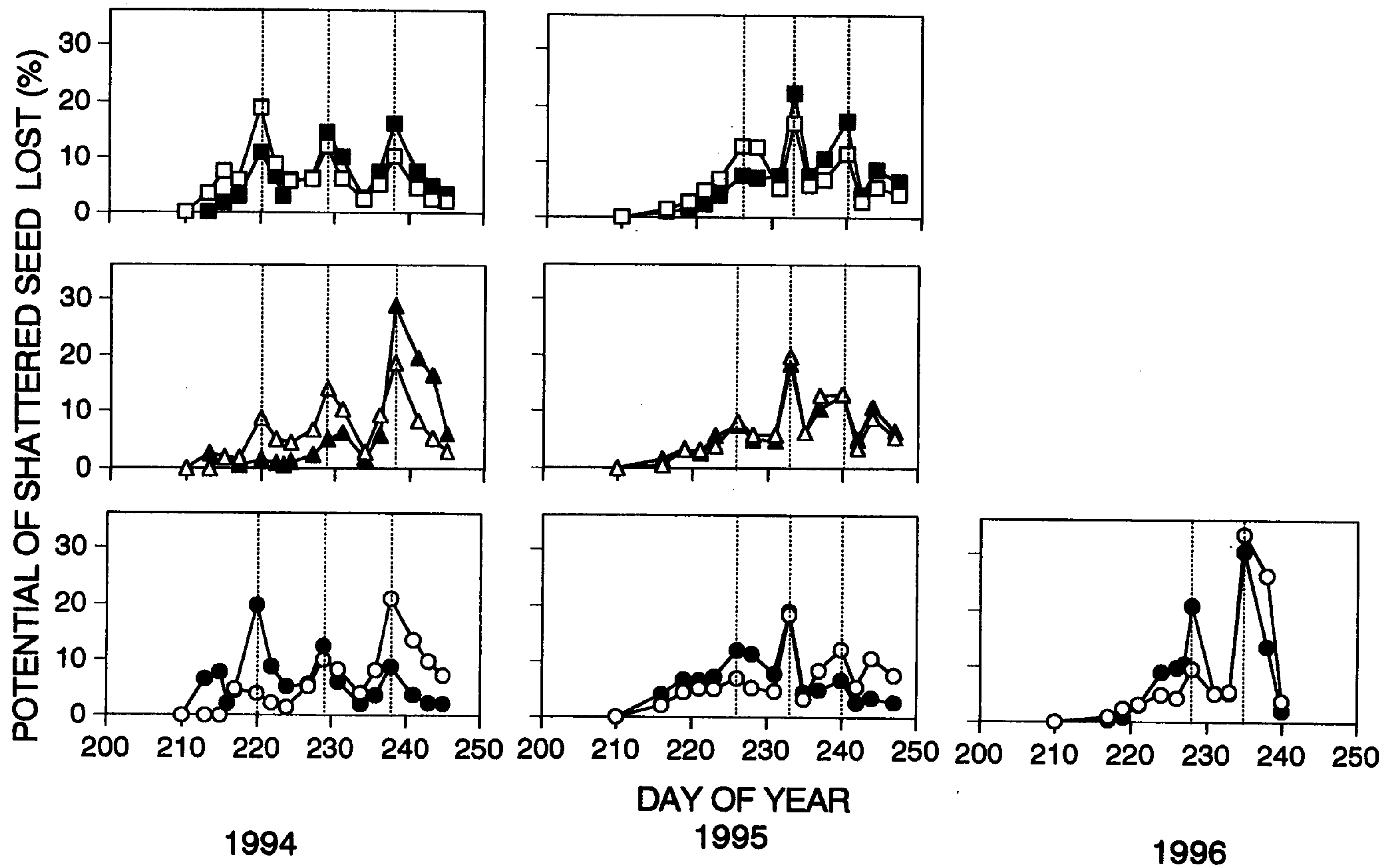

Figure 5.1. Percentage of the total shattered seeds relative to seeds lost at harvest time of birdsfoot trefoil for six irrigation treatments in 1994 and 1995, and two treatments in 1996. Symbols indicate: D30-F50 □, D30-F100 ■, D60-F50 △, D60-F100 ▲, LS ○, C ●. Dashed vertical lines indicate the times of peak shattering events.

generally advanced in the higher water-stress treatment levels in these years also.

Peak flowering is used as a reference plant stage of development because of the variation in time of flowering that may occur among individual genetic clones in the population. Plants grown under non-irrigated conditions exhibited initial peak flowering on DOY 189, 194 and 196 in 1994, 1995, and 1996, respectively. Based on the 1996 non-irrigated treatment results, the number of accumulated HU for the period from the time of peak flowering to the time of initial seed shatter is 238 HU. The length of the flowering period is longer for plants grown under low water-stress conditions (Chapter 4) which results in a longer pod development period which increases the duration of seed shatter loss. Flowering may be delayed when plants are grown in low water-stress conditions because of space competition between vegetative and reproductive structures (Li and Hill, 1989).

The $SS_{\% h}$ peaks for all treatments coincide within years of production and are not altered by crop-water stress status (Fig. 5.1). The number of HUs accumulated between the time from initial flowering to initial pod dehiscence is 381, 383, and 362 for plants grown under LS conditions, and 340, 383, and 362 HUs for plants grown under the non-irrigated treatment conditions, in 1994, 1995, and 1996, respectively. With the exception of treatment C in 1994 that had earlier seed shattering (DOY 213), all treatment and years had similar initial flowering and initial seed shatter times. The period of initiation ranged from DOY 181-183 to 216-217 and the number of days ranged from 34 to 36 days.

Climatic conditions differed among the three years of study (Fig. 5.2). Seasonal fluctuation in T, RH, and VPD coincided with some of the peak shattering events, but no consistent correlations were found between the measures of seed shatter and the climatic data. Multiple regression analyses also did not produce consistent results among irrigation treatments and seed production years (data not shown). The absence of clear relationships between

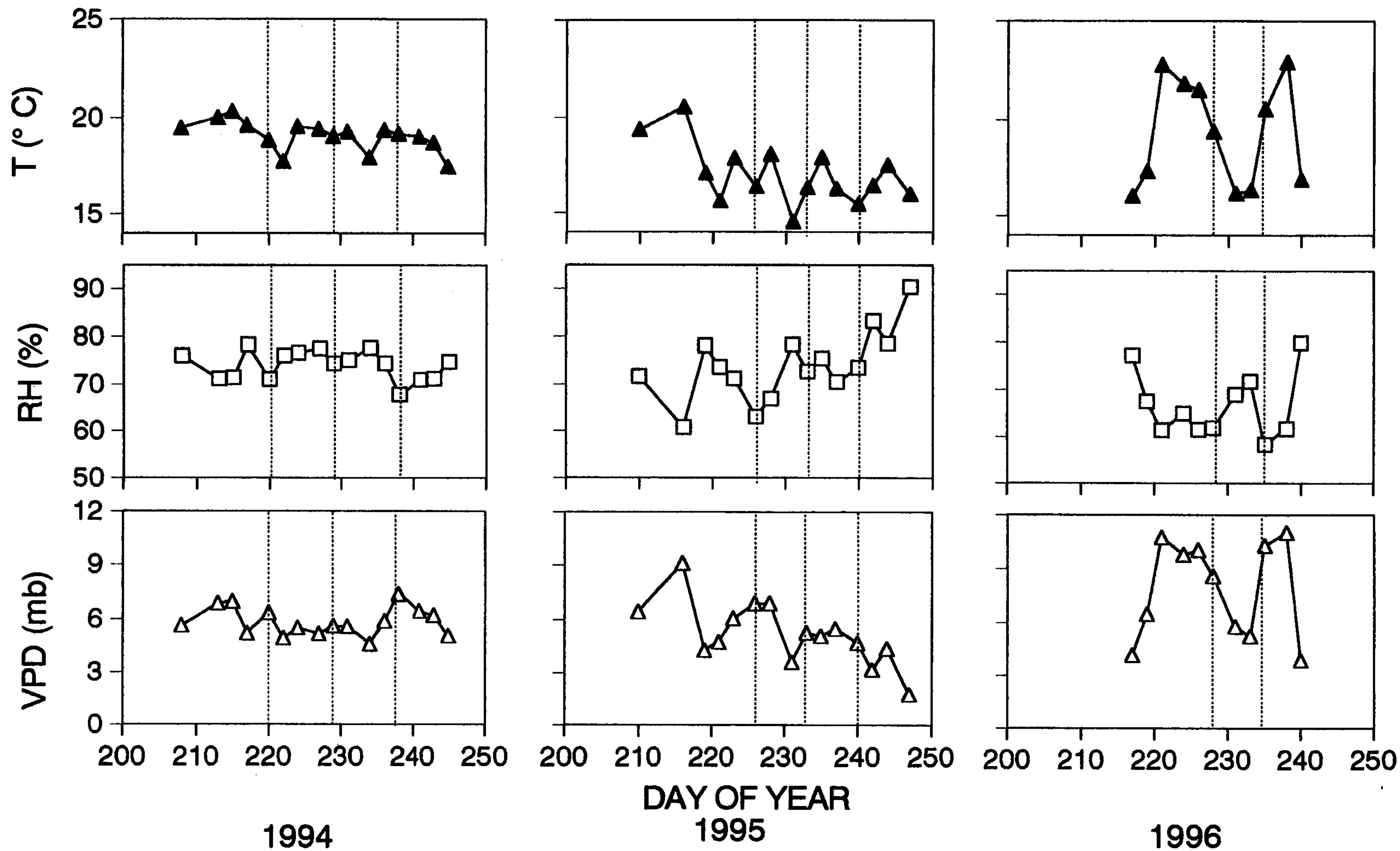

Figure 5.2. Variation in average temperature (T, ▲) , relative humidity (RH, □), and water vapor pressure deficit (VPD, △) in 1994, 1995 and 1996. Dashed vertical lines indicate times of peak shattering events based on the results presented in Fig. 5.1.

seed shattering events and climatic variables may be a result of the indeterminate flowering habit of birdsfoot trefoil. However, because of the similarity in $SS_{\% h}$ peak times for all treatments, it appears that pod dehiscence is regulated by factors other than the water application treatments.

Harvest Time and Seed Shatter Losses

The time of seed harvest differed among treatments (Chapter 3) and was dependent upon the amount of water applied ($r = 0.86$; $P \leq 0.001$). The time of seed harvest in 1994, 1995, and 1996 for the non-irrigated control was DOY 216, 220, and 227, respectively. Cumulative seed losses are related to the cumulative number of pods that shatter, but are affected by the year of production and irrigation treatment (data not shown). The initial rate of pod shattering is more rapid in the non-irrigated control than the LS treatment in all three years (Fig. 5.3).

The number of days from the time of peak flowering until harvest in this experiment ranged were 27, 26, and 31 days (1994, 1995, and 1996, respectively) with corresponding seed shatter losses of 11, 9, and 35% at harvest time (Fig. 5.3). Birdsfoot trefoil seed maturity is reported to occur from 27 to 35 days after full bloom (Anderson, 1955 and Li and Hill, 1989, respectively). If harvest time is based on maximal inflorescence number, then optimal harvest time in this experiment would be 4 to 8 days advanced from that reported for New Zealand conditions (Li and Hill, 1989). The wide range in days to optimal harvest time indicates that harvest-timing based on calendar days is not sufficient to determine a harvest time that will avoid seed shatter losses. Based on theory that successive mechanical processes related to pod drying result in pod dehiscence (Buckovic, 1952; Fahn and Zohary, 1955), climatic conditions are assumed to influence the time of shattering.

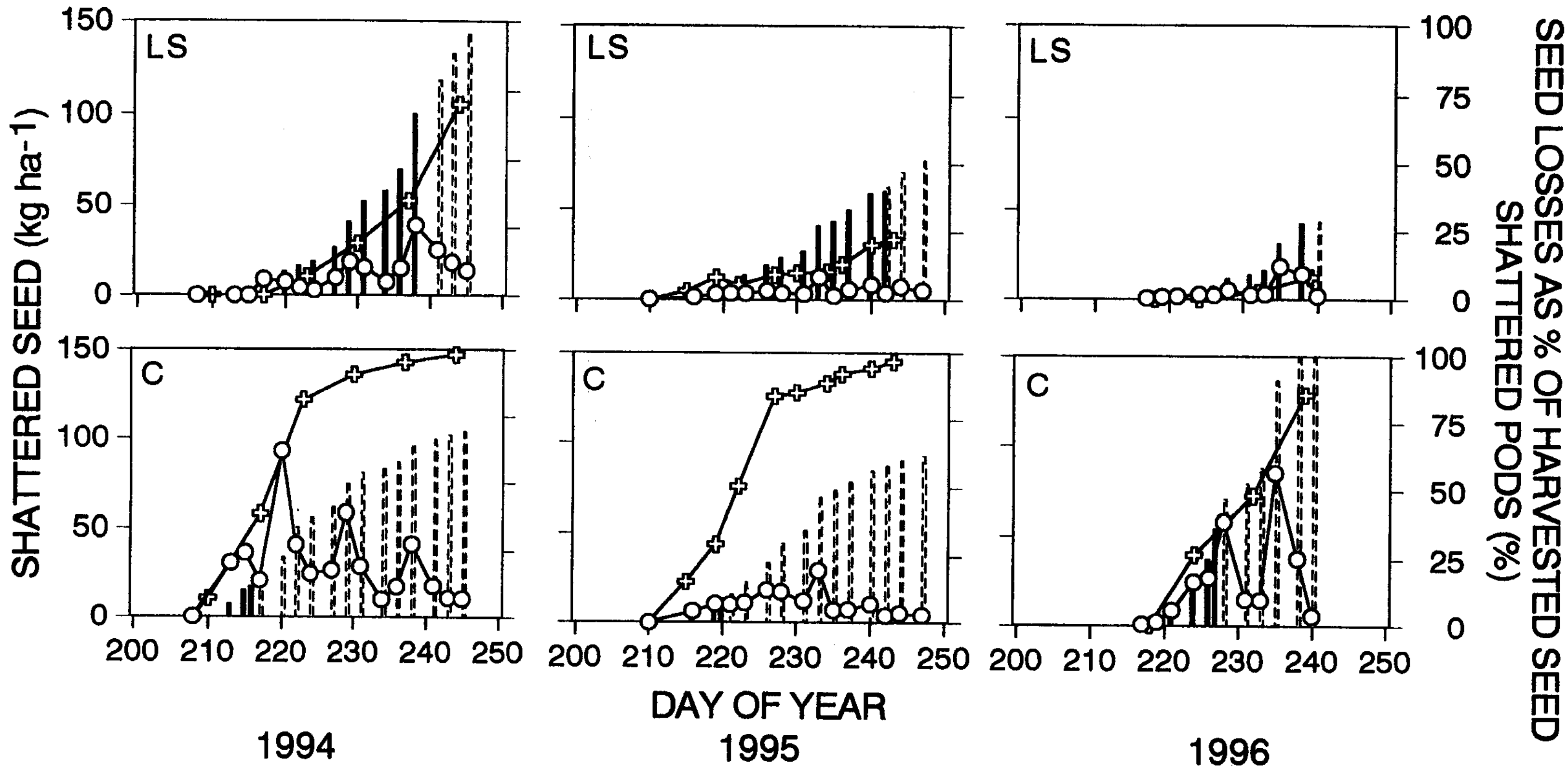

Fig. 5.3. Shattered seeds (O), shattered pods (%) (✚), and seed losses before (■) and after (⊓) harvest time as a percentage of actual harvested seeds from low stressed (LS) and non-irrigated (C) birdsfoot trefoil irrigation treatments in 1994, 1995, and 1996. Harvest time was when the color of most pods were light-tan to brown, the number of mature unshattered pods had reached a maximum, and seed shattering had begun.

The percentage of dehisced pods at harvest time in the non-irrigated control was 38, 36 and 35%, respectively (Fig. 5.3). For the LS treatment, the harvest dates in 1994, 1995, and 1996 were DOY 238, 241, and 238, with the percentage of dehisced pods at harvest time being 36, 20, and 7%, respectively.

The calculated number of accumulated HU from the time of peak flowering until the initial pod dehiscence is 238 HU. A total of 109 HU are needed from the time from initial pod dehiscence until rapid shattering occurs which is approximately 11 days (average daily HU equals 9.5 HU). Delayed harvest time significantly reduces birdsfoot trefoil seed yield (MacDonald, 1946; Anderson, 1955). Harvested seed yield (SY_h) is maximal when the rate of pod maturation is greater than the rate of accumulating dehiscent pods. As maximal SY_h is reached, seed shatter losses to pod dehiscence cannot be reduced by earlier harvest because the number of mature pods harvested will be reduced. When harvested after the time of maximal SY_h, seed yield will always decline because of the increasing rate of dehiscing pods with the accompanying shattered seed losses.

The average rates of pod dehiscence in the non-irrigated control and LS treatments are 5.7 and 1.9% per day. These results agree with previously published results for birdsfoot trefoil of 5 to 71% after 12 days (Anderson, 1955). In *Lotus uliginosus*, pods shattering at a rate of 10% per day resulted in seed yield losses ranging from 7 to 88% (Hare and Lucas, 1984). Comparing the LS and non-irrigated control treatments, the average loss per day of seed yield to pod dehiscence is 3 and 5.3 kg ha^{-1}, respectively.

Conclusions

The total amount of shattered seeds is influenced by irrigation treatment and was correlated with total harvested seed yield. Manipulation of the reproductive development pattern by different water application times and amounts has a significant affect on harvested seed yield, but crop-water stress status affects the percentage of total shattered seeds shattered at harvest time. Increasing amounts of applied irrigation water increase the percentage of the seed crop that will shatter by the time of harvest.

Seed shatter losses fluctuate during the reproductive development period and are not influenced by the different water application treatments. Fluctuations are also observed for climatic variables, but these cannot be used to predict the time of seed shatter events.

The calculated number of accumulated HU from the time of peak flowering until the initial pod dehiscence is 238 HU. A total of 109 HU are needed from the time from initial pod dehiscence until rapid shattering occurs which is approximately 11 days. The average rates of pod dehiscence range from 1.9 to 5.7%, depend on irrigation treatment. The average seed yield loss per day to pod dehiscence is 3 to 5.3 kg ha^{-1}.

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APPENDIX

Apendix Table 1. Annual daily precipitation and temperature data during the1993-94, 1994-95, and 1995-96 growing seasons at Hyslop Farm, Corvallis, OR.

Month	Precipitation			Temperature		
	1993-94	1994-95	1995-96	1993-94	1994-95	1995-96
	---------- mm ----------			---------- °C ----------		
September	2 (-20)	23 (+1)	80 (+58)	13.4 (-3.4)	18.1 (+1.3)	18.0 (+1.2)
October	27 (-39)	98 (+31)	101 (+34)	4.2 (-7.9)	11.1 (-1.0)	11.7 (-0.4)
November	26 (-152)	229 (+50)	196 (+17)	3.8 (-3.9)	4.8 (-2.9)	7.7 (+0.0)
December	203 (+70)	159 (+26)	257 (+124)	6.3 (+3.0)	-10.6 (-13.9)	5.6 (+2.3)
January	99 (-29)	251 (+123)	263 (+135)	6.3 (+1.9)	6.6 (+2.2)	5.7 (+1.3)
February	142 (+26)	109 (-7)	346 (+230)	5.3 (-0.6)	8.0 (+2.2)	5.6 (-0.2)
March	88 (-14)	120 (+18)	90 (-12)	9.7 (+1.1)	8.3 (-0.3)	8.6 (+0.0)
April	49 (-25)	134 (+60)	125 (+510)	10.9 (+0.1)	9.5 (-1.3)	11.2 (+0.4)
May	28 (-32)	36 (-24)	101 (+41)	14.0 (+0.9)	14.2 (+1.0)	11.8 (-1.3)
June	48 (+6)	60 (+18)	22 (-20)	15.3 (-1.1)	16.5 (+0.1)	15.7 (-0.7)
July	1 (-18)	13 (-5)	23 (+5)	20.0 (+1.0)	20.3 (+1.3)	21.0 (+2.0)
August	0 (-12)	21 (+9)	4 (-8)	18.9 (-0.6)	18.3 (-1.2)	20.0 (+0.5)
Total	712 (-241)	1254 (+301)	1608 (+655)			
Average				10.7 (-0.8)	10.4 (-1.0)	11.9 (+0.4)

Numbers within parentheses indicate departures from normal values for the previous 10 years.