# PRODUCTION AND PHYSIOLOGICAL RESPONSES OF ALFALFA TO HARVEST MANAGEMENT AND TEMPERATURE

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PRODUCTION AND PHYSIOLOGICAL RESPONSES OF ALFALFA TO HARVEST MANAGEMENT AND TEMPERATURE

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# PREFACE

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# CHAPTER I

## GENERAL INTRODUCTION

Alfalfa (Medicago sativa L.) is currently produced on over 200,000 hectares in Oklahoma, generating more than $100 million annually from the sale of hay and seed. Alfalfa is an intregral component of the animal feed rations in the state. Since alfalfa is an expensive and difficult crop to establish most years throughout the Southern Plains, it is essential for producers to maintain a healthy, productive stand for as many years as possible. Proper management practices are necessary to maintain a vigorous plant population and a high level of forage production. Alfalfa is a versatile crop adapted to a wide range of environmental conditions.

Alfalfa is generally produced and fed for its protein content, making it a significant factor in ration balancing. Several pre-harvest factors influence the potential feed value such as growth stage, disease and insect damage, cultivar and environmental variations. The main objective of managing a stand of alfalfa is to obtain high yields of quality herbage while maintaining a vigorous and productive plant population.

Several researchers have stated that carbohydrates are the primary energy reserve compounds in plants (Kramer and Koslowski, 1979). Smith and Marten (1970) stated that carbohydrates are utilized by the alfalfa plant for respiratory substrates, structural components, new root

development, regrowth during spring, and production of new photosynthetic tissue if defoliation occurs. The nonstructural carbohydrates stored in the roots of alfalfa serve as a reservoir of carbohydrates available to the growing alfalfa plant. Pearce et al. (1969) reported that alfalfa used the majority of its accumulated carbon compounds during the two weeks following forage harvest. Smith and Marten (1970) found labeled carbohydrates initially stored in the root and crown were readily redistributed to developing shoots. The greatest redistribution occurred at the early vegetative stage and transport decreased with maturity. As photosynthetic capacity increased, the shoot became less and less dependent upon previously stored root reserves.

Fall Harvest Management of Alfalfa

Depletion and replacement patterns for root nonstructural carbohydrates in alfalfa under differing management practices and environmental conditions have been described by many researchers (Reynolds, 1971; Robison and Massengale, 1968; Chatterton et al., 1974). A general recommendation has been to refrain from cutting alfalfa during the four to six weeks prior to the first killing frost in the fall according to Smith (1972), who states that leaf growth is needed during this critical autumn period to synthesize carbohydrates for storage in root and crown tissues. Investigations in northern states have shown a correlation between late autumn (1 October) cutting and subsequent winter injury that resulted in yield reductions and reduced plant populations (Twamley, 1960; Smith, 1968). September 1 harvests actually appeared more detrimental to plant vigor and subsequent spring regrowth than October harvests. Apparently, plants became dormant before

utilizing stored reserves when cut in October. Dexter (1964), Parsons and Davis (1960), and Smith (1962) also found September harvests to be detrimental to stand persistence and yield. Vegetative regrowth resulted in initial root reserve depletion leaving insufficient time to recharge the stored reserves before seasonal growth terminated.

Studies from southern states have shown less evidence of the need for a critical fall "rest" period. Mays and Evans (1973) reported a slight depression in root carbohydrate concentration for two to four weeks following all seasonal cuttings in northern Alabama, but late season cutting treatments were not detrimental to total yield or stand persistence for a well adapted variety. However, yields and stands for less adapted varities were reduced by any cutting after 1 August. These researchers found that fall harvesting in Alabama was more detrimental to 'Dupuits', a wilt-susceptible cultivar, than to 'Williamsburg', a wilt-resistant cultivar. A well adapted alfalfa variety could tolerate a wide range of fall management schedules in a climate typified by northern Alabama.

In Tennessee, Reynolds (1971), did not find a significant positive correlation between total nonstructural carbohydrates (TNC) levels and subsequent forage yields of the 'Buffalo' cultivar after fall harvesting for two years. Jung et al. (1969) in West Virginia; Reynolds (1971) in Tennessee; and Sholar et al. (1983) in Oklahoma also reported no appreciable differences in winter survival or yield in subsequent years following a cutting during the late fall critical period. Edmisten et al. (1988) found stand density unaffected by fall harvest timing in Virginia. The growth period prior to final fall harvest was considered more crucial to alfalfa plant health. Researchers from the southern

states suggest that this lack of correlation between TNC concentrations and forage yields results from the presence of green leaf tissue during winter months enabling photosynthetic activity to continue replenishing reserve materials.

Recent research in the northern states also challenges the fall harvest critical period theory. Tesar and Yagar (1985) reported no decrease in yield or stand persistence when several alfalfa varieties were evaluated after three years of cutting during September or early October in Michigan. The levels of total available carbohydrates (TAC) in the roots of fall cut 'Vernal' or 'DuPuits' cultivars were similar regardless of fall cutting date and were adequate for satisfactory winter survival and persistence. Tesar and Yager (1985) concluded that the interval of time between the second and third cuttings has a more critical effect on winter survival and production than the calendar date of the third and final cutting. These same researchers had reported no significant yield reduction in Vernal or DuPuits alfalfa varieties when cut for the third time on 15 September or 1 October compared to the recommended third cutting on 1 September (Yager and Tesar, 1968). Marten (1980) reported similar results with Vernal alfalfa in Minnesota. He concluded that harvesting the third cutting in September or early October allowed for good persistence and high yields in northern states, provided that soil fertility was adequate, winterhardy cultivars were planted, and adequate snow cover prevailed during the coldest parts of the winter.

Harvesting alfalfa in late fall and grazing in winter have been shown to be possible methods of utilizing fall growth without apparent reductions of future productivity or stand retention. However, an

additional benefit of removing the fall growth is the reduction of overwintering habitat and ovipositional sites for adult alfalfa weevils, (Hypera postica Gyllenhal), which tend to favor areas with abundant plant growth (Dively, 1970; Dowdy et al., 1986). The alfalfa weevil is the most widespread and serious foliage-feeding pest of alfalfa in Oklahoma (Berberet et al., 1981). As a result of reduced oviposition, peak larval populations are likely to be lower as well. Reducing numbers or delaying the occurrence of peak larval populations may result in yield savings and reduced control costs (Berberet et al., 1981).

Spring Harvest Management of Alfalfa

Growth stage at cutting, cutting interval, and spring and fall harvest management have been evaluated by Smith (1972) as important considerations for increasing the potential forage yield, quality and persistence of alfalfa. Investigations of cutting schedules based on stage of development have shown that harvesting at 10% bloom is the best compromise for acceptable forage yield, nutrient value, and stand vigor. Viewpoints on the management of alfalfa have changed with increasing knowledge of the plant's potential to produce and persist under different harvesting schemes. The primary objective of early research studies was to produce the highest possible herbage yields, whereas, more recent research emphasizes feed value. One approach to enhancing hay quality is earlier cutting.

Initial studies of early spring cutting primarily involved cultivars lacking resistance to disease and tolerance to environmental stress (Smith, 1972). Researchers in Wisconsin (Smith, 1968) and Washington (Jackobs, 1952) found that early spring cutting of alfalfa (10 to 30 cm. tall) reduced herbage, protein, and total digestible

nutrient (TDN) yields. In the southern plains of Oklahoma, Graumann et al. (1954) reported that cutting alfalfa at the prebud stage reduced yield, stand persistence, and encouraged weed encroachment. However, Latheef et al. (1988) recently reported that first harvest timing did not adversely affect seasonal or total forage dry matter production, persistence or weed infestation on established, adapted cultivars during a six year study in Oklahoma. Twamley (1960) found while studying differing cutting schedules with four alfalfa cultivars that the cultivar containing both disease resistance and winterhardiness performed well under all harvest schedules in Ontario, Canada. Brink and Marten (1983) reported higher hay yields when alfalfa was cut at prebloom with three additional harvests compared to other harvest schedules in Minnesota.

Temperature and Daylength Effect on Carbon Dioxide Exchange Rates in Alfalfa

Photosynthetic responses of alfalfa to temperature have been studied only to a limited extent. Pearson and Hunt (1972) observed similar net photosynthetic rates in Vernal alfalfa (15 to 20-day-old seedlings with about 10 $cm^2$ leaf area) grown in a cool (20/5 C) and a warm (30/25 C) regime. Chatterton and Carlson (1981) found that the rate of TNC accumulation, the concentration of TNC and carbon dioxide exchange rate (CER) were higher in leaves of alfalfa plants grown in a 10 hour photosynthetic period than in a 14 hour period. Genotypes in this study were selected for either high or low herbage yield and subjected to high (29/24 C) and low (20/15 C) temperatures and two photosynthetic periods (10 and 14 hours). High yielding genotypes produced significantly more herbage than low yielding genotypes in the

14-hour period at 29/24 C. At 20/15 C in both 10 and 14-hour photosynthetic periods the low yielding genotypes produced more herbage than the high yielding genotypes. These values agree with the results for soybeans reported by Chatterton and Silvius (1979).

The potential forage yield and TNC levels in leaves of alfalfa cultivars vary with environmental conditions (Ueno and Smith, 1970; Delaney et al., 1974; Smith and Struckmeyer, 1974). Smith and Struckmeyer (1974) reported a higher concentration of starch in alfalfa leaves grown in cool (20/12 C) rather than warm (30/30 C) day/night temperatures. The cool temperatures presumably resulted in a reduction of photosynthate translocation. Chatterton and Silvius (1979, 1980) observed an acclimation in the rate of starch synthesis when soybean plants (Glycine max L.) grown in one photosynthetic period are shifted to another.

Mays and Evans (1973) suggested that cool, sunny weather combined with the slow growth rate of alfalfa in October and November might enhance stable root TNC levels in the southern states. Sholar et al. (1983) also suggested that the combination of adequate leaf area to actively assimilate $CO_2$ and proper environmental conditions may be responsible for similar root TNC concentrations among the different fall cutting treatment dates. Edmiston and Wolf (1988) suggested the insignificant TNC losses following late fall harvests in Virginia resulted from slow regrowth rates, low respiration rates and relatively high photosynthetic rates during cool autumn temperatures. One further consideration may be the level of dormancy of southern cultivars. Newer semi-dormant cultivars, widely grown in the southern states, may possess enough residual leaf area combined with an assimilate production

mechanism which responds quickly enough to build and maintain appreciable reserve levels during the winter whenever temperature reaches the threshold for alfalfa growth (ie. during periods of short duration when $CO_2$ assimilation by the plant is potentially feasible).

Consequently, to achieve maximum yield and plant persistence a rapid rate of $CO_2$ assimilation is highly desirable. Delaney and Dobrenz (1974) observed a strong positive association between yield and total $CO_2$ uptake per plant. However, Chatterton and Carlson (1981) reported that photosynthesis, as measured by single leaf $CO_2$ exchange rate, was not positively correlated with herbage yield under various controlled environmental conditions.

Delaney et al. (1974) reported a reduction of forage yield in non-dormant alfalfa varieties, as well as a maximum decrease of 38% in apparent photosynthesis and a 19% decrease in dark respiration during periods of high temperature. Robinson and Massengale (1968) found a similar summer decline in forage yield and plant persistence, which was attributed to increased respiration with high night-time temperatures. These results suggest that photosynthetic efficiency during periods of high temperature has a greater effect of alfalfa forage yield than dark respiration. These same researchers also noted the concentration of carbohydrates in alfalfa roots also declined, indicating that food materials were not assimilated fast enough for plant utilization and replenishment to root materials during periods of high night temperature.

The results of these studies suggest that carbohydrate accumulation, persistence, and yield may be related to the $CO_2$ assimilation rate of alfalfa cultivars during periods of stressful

growing conditions. Yield potential, photosynthetic response, and TNC concentrations reportedly fluctuate with environmental conditions (temperature and photosynthetic period) among genotypes. The plant's reaction to $CO_2$ assimilation and carbohydrate storage may vary with level of dormancy and this may also be a factor which determines persistence of the crop stand and subsequent yield. This could help explain why some alfalfa cultivars harvested during the "critical period" are not adversely affected.

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# CHAPTER II

## SPRING AND FALL HARVEST MANAGEMENT EFFECTS ON ALFALFA PRODUCTION, QUALITY, AND STAND PERSISTENCE IN NORTH CENTRAL OKLAHOMA


## ABSTRACT

Early spring (early bud) harvesting of alfalfa (Medicago sativa L.) has potential for increasing forage quality and reducing damage by the alfalfa weevil (Hypera postica Gyllenhal) in some areas. However, first harvest yields will likely be lower when alfalfa is cut in a prebloom growth stage. Late fall harvesting of alfalfa forage may result in increased forage utilization and decreased pest habitat. However, the potential for plant injury due to late harvest has been demonstrated.

The objective of this research was to determine the effects of these two harvesting schedules individually and in combination on root total nonstructural carbohydrate (TNC) concentrations, forage production, forage quality and stand persistence of alfalfa. Cultivars of differing dormancy levels were used to provide a range of spring and fall growth patterns which may interact with harvest treatments to affect measured responses. Field experiments were conducted in 1987 and 1988 under nonirrigated conditions at the Perkins Experiment Station and in 1988 under irrigated conditions at the Stillwater Experiment Station.

Four harvest management regimes were imposed on four alfalfa cultivars ('Advantage,' 'WL-320,' 'Baron,' and 'Pioneer 5929') that differ in level of dormancy from high to low, respectively.

Harvest treatments were: control (harvest at the 10% bloom growth stage with a six week growth period prior to fall dormancy), fall (control plus an additional harvest during the fall growth period), spring (control plus an additional harvest in early spring at the early bud growth stage), spring/fall (a combination of the spring and fall harvest schedules). All mid-season harvests were made at 10 to 25% bloom. Forage yields were measured for each treatment and cultivar combination at each forage harvest. Samples of the first, third and last seasonal harvests were analyzed for protein content. Root carbohydrate analyses were conducted on samples collected during mid-winter dormancy and persistence measurements were taken by undercutting yield plots after the first harvest of 1989.

Total dry matter yield was significantly lower in the spring and spring/fall harvest management treatments for the first year only on the rainfed plots. Total dry matter yield did not differ the second year even though first harvest yields were significantly lower with early spring harvests because an additional cutting was possible during the mid-season for these treatments. The Advantage and WL-320 cultivars with the greater level of dormancy maintained the highest yields over all harvest treatments. The least dormant cultivar, Pioneer 5929, had a higher TNC concentration in midwinter after the first season. After two harvest seasons TNC levels of cultivars averaged over all treatments were not significantly different. Alfalfa root TNC concentration

averaged over all cultivars was lower with the fall and spring/fall harvest treatments after the second year. No interaction was evident between cultivar and harvest treatments for total dry matter yield or root TNC levels at either location. No consistent relationship was apparent between root TNC levels and seasonal or first harvest yield.

Since no consistent relationship could be found between root TNC levels and seasonal or first harvest yield after two harvest seasons, the data indicate that TNC levels may not be affected to a detrimental level in this environment. Consequently, a producer may have more harvest alternatives available to control the alfalfa weevil populations without a decline in seasonal forage production. However, the cost of harvesting the extra cuttings must be evaluated to determine feasibility. Additional harvests were required to make up for the lower yield from early spring cuttings.

# INTRODUCTION

A depletion and replacement pattern for nonstructural carbohydrates in alfalfa (Medicago sativa L.) roots under differing management practices and environmental conditions has been described by many researchers (Reynolds, 1971; Robison and Massengale, 1968; Chatterton et al., 1974). Carbohydrates stored in alfalfa roots are utilized by the plant for respiratory substrates, structural components, new root development, initial growth and subsequent rapid growth during the spring, and maximum production of new photosynthetic tissue when defoliation occurs (Smith and Marten, 1970). Harvest timing and frequency has been reported to affect yield and stand longevity of alfalfa (Kust and Smith, 1961; Robison and Massengale, 1968; Brink and Marten, 1983). A general recommendation has been to refrain from cutting alfalfa during the four to six weeks previous to the first killing frost in the fall (Smith, 1972). Leaf growth is needed during the autumn period to synthesize carbohydrates for storage in root and crown material. Investigations in northern states have shown a correlation between late fall cutting and subsequent winter injury, resulting in yield reductions and reduced plant populations (Twamley, 1960; Smith, 1968). They showed that September harvests were more detrimental to plant vigor and subsequent spring regrowth than October harvests, reasoning that plants became dormant before utilizing stored reserves with later harvests.

The majority of early research projects relating to effects of variable harvest schedules were conducted in the more humid, northern areas of the United States. Less attention has been given to alfalfa management in fluctating environmental conditions prevalent in the

management in fluctating environmental conditions prevalent in the Southern Plains. Latheef et al. (1988), reported that early harvest (pre-bloom stage of growth) can be utilized in Oklahoma as a pest management practice and to obtain higher quality forage without reducing the productive life of alfalfa stands. Sholar et al. (1988) found no effects on root TNC, yield, or plant and stem densities attributable to late fall harvest schedules in three cultivars studied in Oklahoma. However, no studies have evaluated the combined effects of both early spring and late fall harvest treatments or the effect of these harvest schemes on alfalfa cultivars with differing genetically inherent dormancy levels.

Numerous studies have addressed the effects of early cutting on alfalfa production. Latheef et al. (1988) reported that first harvest timing did not adversely affect seasonal or total forage dry matter production, alfalfa stand persistence or weed infestation in Oklahoma. Brink and Marten (1983) reported higher hay yields when alfalfa was cut at the prebloom growth stage followed by three additional harvests in Minnesota. However, several researchers in the northern climates of Wisconsin and Washington found that early spring cutting of alfalfa (10 to 30 cm tall) reduced herbage, protein, and TDN yields (Smith, 1968; Jackobs, 1952). In the Southern Plains of Oklahoma, Graumann et al. (1954) reported that cutting at the prebud stage reduced yield, stand persistence, and encouraged weed encroachment.

Results from early work are largely based upon cultivars lacking resistance to disease and tolerance to environmental stress (Smith, 1972). Twamley (1960) found while studying different cutting schedules with four alfalfa cultivars that the one having both disease resistance

and winterhardiness performed well under all harvest schedules at Ontario, Canada.

Mays and Evans (1973) found that fall harvesting in Alabama, was more detrimental to 'Dupuits', a wilt-susceptible cultivar, than 'Williamsburg', a wilt-resistant cultivar. Mays and Evans (1973) concluded that a well adapted alfalfa variety could tolerate a wide range of fall management schedules in a climate typified by northern Alabama. Jung et al. (1969) in West Virginia; Reynolds (1971) in Tennessee; and Sholar et al. (1983) in Oklahoma also reported no appreciable difference in winter survival or subsequent yield following a cutting during the late fall critical period. In Tennessee, Reynolds (1971), did not find a significant positive correlation between TNC levels and subsequent forage yields of the 'Buffalo' cultivar after fall harvesting for two years. These researchers from the southern states suggest that this lack of correlation between TNC concentrations and forage yields results from the presence of green leaf tissue during winter months enabling photosynthetic activity to continue replenishing reserve materials.

Recent research in the northern states also challenges the fall harvest critical period theory. Marten (1980) found no decline in spring forage yields and no detrimental effect on stand persistence following a late harvest when winterhardy cultivars are grown on fertile soil. Tesar and Yagar (1985) also reported no decrease in yield or stand persistence when several alfalfa cultivars were evaluated after three years of cutting during September or early October in Michigan. The levels of total available carbohydrates (TAC) in the roots of fall

cut 'Vernal' and DuPuits cultivars were similar regardless of fall cutting date and were adequate for satisfactory winter survival and persistence.

The objective of this research was to determine the effects of differing spring and fall management schemes on yield, root TNC concentrations, forage quality, and stand persistence of alfalfa cultivars varying in dormancy levels in Oklahoma.

## MATERIALS AND METHODS

Four alfalfa cultivars, selected for a range of high to low dormancy characteristics, were grown at two locations in Payne County, Oklahoma. Soil at the Stillwater location consists of a Ashport Fine-silty, mixed, thermic Fluventic Haplustoll, while the Perkins location has a Navina Fine-loamy, mixed, thermic Udic Argiustoll (0 to 1% slope). Plots were seeded at a rate of 22.4 kg/ha on October 15, 1986, at Perkins and October 15, 1987, at Stillwater. Fertilizer and lime were incorporated at the recommended rates and pesticides were applied as needed. Carbofuradan insecticide and pronamide herbicide was applied prior to the first seasonal harvest for alfalfa weevil and weed control. Experiments were conducted in 1987 and 1988 under rainfed conditions at Perkins and under irrigated conditions in 1988 at Stillwater.

Plots were arranged in a randomized complete block design with a split plot factorial arrangement of four harvest management regimes as main plots with four cultivars ('Advantage', 'WL-320', 'Baron' and 'Pioneer 5929') as subplots. Harvest treatments were: control (harvest at the 10% bloom growth stage with a six week rest period prior to fall dormancy), spring (control plus an early bud growth stage harvest in the early spring), fall (control plus an additional harvest during the late season growth period), spring/fall (a combination of the spring and fall harvest schedules). Plot dimensions at Perkins were 2 m x 5 m, including a 1 m x 5 m area harvested for yield estimates and the remaining 1 m x 5 m was used for root sample excavation. Plot dimensions at Stillwater were 1 m x 6 m with a 1 m x 5 m strip used for yield estimates and the remaining 1 $m^2$ used for root sample excavation.

Forage yields were recorded for all harvests using a flail harvester and forage quality samples were collected for the first, third, and last harvests at both locations. Clipping height was approximately four cm. A sample of approximately 250 grams (fresh weight) was collected at each harvest from each plot and dried at 65 C for dry matter yield determination.

Root TNC reserves were measured from alfalfa roots excavated after the initial killing freeze (-5 C) each fall. Roots from 20 plants per plot were cleaned and dried at 100 C for 90 minutes followed by additional drying at 70 C for 72 hours. A 10 cm section of taproot material directly below the crown was ground through a 2 mm screen prior to grinding through a 0.25 mm screen to ensure uniform particle size. Total nonstructural carbohydrates were extracted using the enzymes amyloglucosidase and amylase for 24 hours at 55 C (Smith, 1981) from 200 mg of root tissue. Reducing sugars were determined spectrophotometrically at a wavelength of 410 nm using a p-hydroxybenzoic hydrazide (PAHBAH) alkaline solution as an indicator (Lever, 1972).

Near infrared reflectance spectroscopy (NIRS) was used to predict alfalfa protein (Lindgren, 1988). Alfalfa forage samples were ground in a UDY Cyclone Mill through a 0.25 mm screen to ensure uniformity. Random samples were evaluated by the Kjeldahl method (Bradford, 1965) for nitrogen determination (adjusted to protein concentration) to support NIRS values. Acid detergent fiber and neutral detergent fiber contents were also evaluated in randomly selected samples by the Van Soest fiber analysis method (Van Soest, 1967).

Final plant densities were determined in May of 1989 at the Perkins Experiment Station. A 0.6 m x 5 m strip in each yield plot was undercut to 15 cm and living taproots counted to compare the relative effects of the imposed harvest treatments and cultivar differences.

# RESULTS

## Total Nonstructural Carbohydrates

Total nonstructural carbohydrate (TNC) levels measured in roots excavated during mid-winter dormancy at Perkins were significantly higher ($P \leq 0.05$) in the least dormant cultivar (Pioneer 5929) when averaged over all harvest treatments in 1987 (Table 1). After two harvest seasons, TNC levels of cultivars averaged over all treatments were not different (Table 1). The two dormant cultivars (Advantage and WL-320) increased in TNC from 1987 to 1988. However, TNC concentrations in the less dormant cultivars (Baron and 5929) decreased slightly from 1987 to 1988. At the Perkins location, the Advantage had relatively high TNC level of 29.8 % while Baron was lowest at 27.3 % in 1988 (Table 1). The first season, TNC concentrations were not different among harvest treatments (Table 1). Alfalfa root TNC concentration averaged over all cultivars was lowest in the fall and spring/fall harvest treatments after the second harvest season ($P \leq 0.05$) (Table 1). Levels of TNC at the Perkins Experiment Station ranged from a high of 35.2% for the spring treatment to a low of 24.6% for the fall treatment in 1988. The spring harvest treatment resulted in greater TNC levels than occurred in the control. No interaction was evident between cultivar and treatment for root TNC levels at this location.

Total nonstructural carbohydrate levels averaged across all harvest treatments were not different among cultivars after the first full harvest season (1988) for the Stillwater Experiment (Table 2). Levels of TNC ranged from a high of 31.9 % for Advantage to a low of 27.9% for Pioneer 5929 that same year (Table 2). Alfalfa root TNC concentration averaged over all cultivars was lower with the fall and spring/fall

harvest treatments compared to the spring treatment after the first harvest season ($P \leq 0.05$) (Table 2). The spring treatment had the highest TNC level of 36.1% for the spring treatment to a low of 26.9% and 26.6% for the fall and spring/fall treatments, respectively, that same year. Again, there was no treatment by cultivar interaction for root TNC levels.

Root TNC values of similar concentrations reported in past research experiments were found to be adequate to survive winter dormancy in northern climates. Root TNC concentrations at both locations were all greater than 24% indicating that carbohydrates may not be the determining factor for winter survival in Oklahoma.

Forage Yield

Seasonal dry matter yield averaged across all cultivars for the Perkins Experiment was significantly affected ($P \leq 0.05$) by the harvest treatments in 1987, but not in 1988 (Table 3). The spring treatments had lower first harvest yields for which there was not adequate compensation during later harvests in 1987. First harvest yield measured after one full season of imposed treatments (Spring, 1988) at this location was significantly reduced compared to the control ($P \leq 0.05$) in the spring and spring/fall harvest schedules (Table 3), attributable to the somewhat limited growth present at the early bud growth stage. The fall management treatment was also significantly lower ($P \leq 0.05$) than the control treatment for the first harvest yields (Table 3).

Total seasonal dry matter yield did not differ the second year with early spring harvest treatments even though first harvest yields were much lower, because an additional cutting was possible during the mid-season for these treatments (Table 4). First harvest yields were

considerably lower in 1989 than the previous year, possibly due to the different growing conditions in the early spring. The two spring harvest treatments including late fall harvest were significantly lower ($P \leq 0.05$) in first harvest yield than the control harvest treatment (Table 3). Total dry matter yield averaged over all harvest treatments for the Perkins Experiment differed among cultivars the first year but not the second (Table 5).

Seasonal forage yields for the Stillwater Experiment were not affected by harvest treatment during 1988 (Table 6) despite differences in first harvest yields (table 6) and an added harvest for the fall and spring/fall treatments (Table 9). The total seasonal yield at this location in 1988 ranged from 22.3 Mg/ha on the control plots to 20.8 Mg/ha for the spring/fall harvest treatment (Table 6). First harvest yields in 1989 after one full season of harvest effects were significantly greater ($P \leq 0.05$) for the control treatment than any other harvest treatment (Table 6).

No cultivar by harvest management interaction was evident for dry matter yield at either location in either year. Even though cultivars varied in growth habit, yield, and persistence, they responded similarly to harvest schedules.

Forage Quality

First harvest forage quality, measured as percent crude protein concentration, was significantly higher in the spring harvest treatments ($P \leq 0.05$) at the Perkins Experiment Station for both years (Table 3). Crude protein concentration was greatest on the early spring cut plots with a high of 18.3% and lowest on the control plots at 16.5% during 1987 (Table 3). Protein concentration was greater on all treatments in

1988 than in 1987 for both first harvest and mid-season samples. No difference in crude protein was detected at the Stillwater Experiment Station at the first harvest in 1988 (Table 6). By mid-season, protein concentrations were highest ($P \leq 0.05$) in the control and fall harvest treatments which had not been cut early in the spring.

Percent Stand Persistence

Final plant root densities for the Perkins Experiment evaluated at the termination of this study were significantly reduced ($P \leq 0.05$) in the least dormant cultivars. Plant densities averaged 27 plants/$m^2$ for Pioneer 5929 compared to 157 plants/$m^2$ for the WL-320 cultivar (Table 10).

Plant population densities on the late fall harvest plots tended to be higher than for the control or spring harvest schedules. The spring harvest schedule had the lowest population density of all treatments. However, population densities were not significantly different ($P \leq 0.05$) when averaged across all cultivars. Plant densities ranged from 112.5 plants/$m^2$ for the fall harvest treatment to 95.8 plants/$m^2$ for the spring harvest treatment (Table 10).

# DISCUSSION

Total nonstructural carbohydrates (TNC) were influenced by management practice at both locations in 1988. The fall and spring/fall management treatments resulted in decreased TNC concentrations when averaged across all cultivars. Fall harvest treatments resulted in lower root TNC levels, which agree with reports from northern climates. Kust and Smith (1961) found root TNC levels of 25% to 26% for alfalfa harvested on 1 October compared to 29% to 30% on plots not harvested during the late fall in Wisconsin. Mays and Evans (1973), Collins and Taylor (1980), and Sholar et al. (1983) found no consistent reduction in TNC levels with late fall harvest studies conducted in southern climates. Sholar et al. (1983) suggested that a combination of proper environmental conditions and available photosynthetic tissues may be responsible for stable TNC levels in late fall harvested alfalfa stands grown in central Oklahoma.

Severe late winter weather caused considerable stand losses to alfalfa in the 1988-89 winter in this environment. First harvest yields in 1989 in this study were quite low as a result. There was some disadvantage for those treatments harvested in the fall of the previous season at both Perkins and Stillwater (Table 3 and 6). Spring or spring/fall harvesting at Stillwater the previous year also lowered first harvest yield compared to controls in 1988. Low first harvest yields in 1989 do relate to lower midwinter root TNC levels in the winter of 1988 at Perkins for the fall and fall/spring treatments (Tables 1 and 3). However the relationship does not hold true at Stillwater where the early spring harvest treatment also showed

decreased first harvest yield but had the highest midwinter root TNC level (Tables 2 and 6).

Levels of TNC did not vary among the four cultivars when averaged across all harvest treatments at the Stillwater and Perkins locations in 1988. Pioneer 5929 was significantly higher ($P \leq 0.05$) in TNC after the first year but did not differ from other cultivars after the second harvest season.

The total number of harvests for the different treatment schedules on dryland alfalfa stands is dependent upon seasonal precipitation patterns. In 1987, the late fall and spring/fall harvest treatments received one extra cutting compared to the control and spring treatments at Perkins (Table 4). Precipitation was seasonally consistent with thirty-year averages resulting in a two month cessation of forage production in the mid-summer after the third harvest for all treatments due to limited available soil moisture (Table 8). Even though the control treatment received fewer harvests, the total seasonal forage production was significantly greater ($P \leq 0.05$) than the spring/fall harvest scheme (Table 3). Precipitation patterns were less consistent with thirty-year averages in 1988 on the Perkins Experiment Station resulting in a limited availability of soil water earlier in the growing season (Table 8). Consequently, the spring and fall harvest treatment schemes received an additional cutting, while the spring/fall treatment received two extra harvests for the season (Table 4). The control treatment was harvested three times compared to the spring/fall treatment receiving five seasonal cuttings. However, there was no significant difference in yield for any harvest scheme under these conditions (Table 3). Forage production ranged from a high of 16.7

Mg/ha for the control treatment to a low of 14.7 Mg/ha in the spring/fall harvest treatment.

The irrigated plots at the Stillwater Experiment Station experienced no seasonal water deficit. For the first harvest season the total dry matter production was not affected by any treatment scheme, even though the fall and spring/fall harvest schemes received one additional late season harvest (Table 6). The dry matter production ranged from a high of 22.8 Mg/ha for the fall treatment to 20.8 Mg/ha for the spring treatment. Total forage dry matter yield for the four cultivars, averaged over all harvest treatments, declined with dormancy rating ($P \leq 0.05$) in 1988 (Table 5).

Since no consistent relationship could be found between root TNC levels and seasonal or first harvest yield after two harvest seasons, the data indicate that TNC levels may not be lowered to a level critical to survival in this environment. Consequently, a producer may have more alternatives available to control alfalfa weevil populations with no decline in seasonal forage production. Some benefits of early spring first harvests are increased forage quality (Smith 1981) and an additional harvest prior to mid-summer drought in some years (Tables 4 and 9). The disadvantages will be the decreased first harvest yields and the extra cost of harvesting. Late fall harvesting may also be advantageous for control of alfalfa weevil habitat during winter months. An additional benefit may also be the competitive survival advantage stimulated by late season harvests (Table 10). Chatterton et al. (1974) also noted a competitive advantage in alfalfa populations harvested just prior to winter dormancy. However, this study did not

support the higher TNC values found by many researchers studying late fall harvest schedules.

After two harvest seasons there was no apparent benefit for any harvest system regarding total seasonal yield under irrigated conditions. However, the cost of harvesting the extra cuttings must be evaluated to determine feasibility. The additional harvests were required to make up for the yield loss from early spring cuttings. Two extra harvests were required to compensate for the early harvests in 1988.

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Table 1. Mid-winter alfalfa root total nonstructural carbohydrate (TNC) concentrations averaged for all cultivars and harvest treatments for the Perkins Experiment.

| CULTIVAR | 1987 | 1988 |
|---|---|---|
| | %TNC | |
| Advantage | 26.7 b | 29.8 |
| WL-320 | 28.0 b | 29.7 |
| Baron | 27.4 b | 27.3 |
| 5929 | 30.2 a | 29.3 |
| LSD(0.05) | 1.9 | NS |
| TREATMENT | | |
| Control | 30.5 | 30.1 b |
| Spring | 30.3 | 35.2 a |
| Fall | 25.1 | 24.6 c |
| Spring/Fall | 26.5 | 26.3 c |
| LSD(0.05) | NS | 3.2 |

Table 2. Mid-winter alfalfa root total nonstructural carbohydrate (TNC) concentrations averaged for all cultivars and harvest treatments for the Stillwater Experiment.

| CULTIVAR | 1988 |
|---|---|
| | ---- %TNC ---- |
| Advantage | 31.9 |
| WL-320 | 28.3 |
| Baron | 31.6 |
| 5929 | 27.9 |
| LSD(0.05) | NS |
| TREATMENT | |
| Control | 30.2 ab |
| Spring | 36.1 a |
| Fall | 26.9 b |
| Spring/Fall | 26.6 b |
| LSD(0.05) | 6.2 |

Table 3. Forage dry matter yields (Mg/ha) and crude protein concentration (%) for all treatments across all cultivars of alfalfa for the Perkins Experiment.

| | TOTAL SEASONAL YIELD | FIRST HARVEST YIELD | PROTEIN | MID-SEASON HARVEST YIELD | TREATMENT PROTEIN |
|---|---|---|---|---|---|
| | | | 1987 | | |
| | Mg/ha | | % | Mg/ha | % |
| Control | 13.7 a | 3.3 a | 16.5 b | 3.0 b | 17.6 |
| Spring | 10.0 b | 2.5 b | 18.3 a | 3.3 b | 18.2 |
| Fall | 12.1 ab | 3.2 a | 16.9 b | 3.1 b | 17.2 |
| Spring/Fall | 11.0 b | 2.5 b | 18.3 a | 3.9 a | 18.0 |
| LSD(0.05) | 2.6 | 0.3 | 0.7 | 0.6 | NS |
| | | | 1988 | | |
| Control | 16.7 | 8.7 a | 17.7 b | 3.2 | 19.3 |
| Spring | 14.7 | 3.6 c | 21.7 a | 3.1 | 18.9 |
| Fall | 15.3 | 7.5 b | 17.0 b | 3.1 | 19.2 |
| Spring/Fall | 14.7 | 3.4 c | 22.0 a | 3.0 | 19.5 |
| LSD(0.05) | NS | 0.9 | 0.8 | NS | NS |
| | | | 1989 | | |
| Control | | 3.5 a | | | |
| Spring | | 3.1 ab | | | |
| Fall | | 2.7 b | | | |
| Spring/Fall | | 2.9 b | | | |
| LSD(0.05) | | 0.5 | | | |

Table 4. Treatment harvest dates at the Perkins Experiment Station.

| 1987 | | | |
|---|---|---|---|
| CONTROL | SPRING | FALL | SPRING/FALL |
| ---- | 4/27 | ---- | 4/27 |
| 5/11 | ---- | 5/11 | ---- |
| ---- | 6/5 | ---- | 6/5 |
| 6/8 | ---- | 6/8 | ---- |
| ---- | 7/8 | ---- | 7/8 |
| 7/15 | ---- | 7/15 | ---- |
| 9/29 | 9/29 | 9/29 | 9/29 |
| ---- | ---- | 11/1 | 11/1 |
| 4 | 4 | 5 | 5 |
| TOTAL NUMBER OF HARVESTS FOR 1987 | | | |
| 1988 | | | |
| ---- | 4/18 | ---- | 4/18 |
| 5/13 | ---- | 5/13 | ---- |
| ---- | 5/26 | ---- | 5/26 |
| 6/10 | ---- | 6/10 | ---- |
| ---- | 6/22 | ---- | 6/22 |
| 10/4 | 10/4 | 10/4 | 10/4 |
| ---- | ---- | 11/10 | 11/10 |
| 3 | 4 | 4 | 5 |
| TOTAL NUMBER OF HARVESTS FOR 1988 | | | |
| 1989 | | | |
| ---- | 4/25 | ---- | 4/25 |
| 5/9 | ---- | 5/9 | ---- |

Table 5. Total forage dry matter yield averaged over all harvest treatments for all cultivars for the Perkins and Stillwater Experiments.

| CULTIVAR | 1987 | 1988 |
|---|---|---|
| | PERKINS EXPERIMENT | --------- Mg/ha --------- |
| Advantage | 12.1 a | 16.7 |
| WL-320 | 12.6 a | 16.7 |
| Baron | 12.8 a | 15.5 |
| 5929 | 9.3 b | 12.6 |
| LSD(0.05) | 2.6 | NS |
| | STILLWATER EXPERIMENT | |
| Advantage | 23.6 b | |
| WL-320 | 24.9 a | |
| Baron | 22.2 c | |
| 5929 | 17.2 d | |
| LSD(0.05) | 1.1 | |

Table 6. Forage dry matter yields (Mg/ha) and crude protein concentrations (%) for all treatments across all cultivars of alfalfa for the Stillwater Experiment.

| | TOTAL SEASONAL YIELD | FIRST HARVEST YIELD | PROTEIN | MID-SEASON HARVEST YIELD | TREATMENT PROTEIN |
|---|---|---|---|---|---|
| | | | 1988 | | |
| | Mg/ha | | % | Mg/ha | % |
| Control | 22.3 | 4.8 a | 19.3 | 2.1 b | 20.3 a |
| Spring | 20.8 | 2.9 b | 20.0 | 3.0 a | 18.9 bc |
| Fall | 22.8 | 3.2 b | 19.4 | 1.9 b | 20.0 ab |
| Spring/Fall | 22.8 | 1.8 c | 19.6 | 3.1 a | 18.5 c |
| LSD(0.05) | NS | 0.8 | NS | 0.4 | 1.2 |
| | | | 1989 | | |
| Control | | 4.8 a | | | |
| Spring | | 2.9 b | | | |
| Fall | | 3.2 b | | | |
| Spring/Fall | | 1.8 c | | | |
| LSD(0.05) | | 0.8 | | | |

Table 7. Thirty-year, annual, and monthly mean precipitation values during harvest management studies at the Stillwater Experiment Station.

| Month | 30 Year Mean | Year | | |
|---|---|---|---|---|
| | 1958-1987 | 1987 | 1988 | 1989 |
| | cm | | | |
| Jan. | 2.3 | 6.4 | 3.6 | 4.2 |
| Feb. | 3.0 | 13.7 | 0.9 | 4.3 |
| Mar. | 5.5 | 8.6 | 13.9 | 9.5 |
| Apr. | 6.7 | 1.6 | 10.7 | 0.4 |
| May | 12.9 | 17.2 | 7.9 | 17.2 |
| Jun. | 10.0 | 17.5 | 3.3 | |
| Jul. | 9.7 | 7.4 | 6.9 | |
| Aug. | 7.1 | 5.4 | 2.5 | |
| Sept. | 9.9 | 11.2 | 19.8 | |
| Oct. | 7.5 | 3.1 | 4.1 | |
| Nov. | 4.6 | 6.7 | 8.9 | |
| Dec. | 3.1 | 9.7 | 2.5 | |
| Annual Total | 82.3 | 108.5 | 85.0 | |
| Deviation from mean | | +26.2 | +2.7 | |

Table 8. Thirty-year, annual, and monthly precipitation values during harvest management studies at the Perkins Experiment Station.

| Month | 30 Year Mean | Year | | |
|---|---|---|---|---|
| | 1958-1987 | 1987 | 1988 | 1989 |
| | | cm | | |
| Jan. | 2.8 | 4.2 | 2.4 | 2.4 |
| Feb. | 3.2 | 10.7 | 1.3 | 4.5 |
| Mar. | 6.1 | 8.2 | 14.1 | 6.9 |
| Apr. | 6.7 | 1.9 | 13.0 | 0.6 |
| May | 13.2 | 18.3 | 7.1 | 21.7 |
| Jun. | 10.6 | 19.7 | 3.1 | |
| Jul. | 9.0 | 3.9 | 6.7 | |
| Aug. | 6.6 | 5.4 | 2.2 | |
| Sept. | 10.7 | 15.6 | 19.6 | |
| Oct. | 8.0 | 2.3 | 3.4 | |
| Nov. | 5.3 | 4.0 | 9.4 | |
| Dec. | 3.4 | 8.7 | 2.8 | |
| Annual Total | 85.7 | 102.9 | 82.1 | |
| Deviation from mean | | +17.2 | -3.6 | |

Table 9. Treatment harvest dates at the Stillwater Experiment Station.

| 1988 | | | |
|---|---|---|---|
| CONTROL | SPRING | FALL | SPRING/FALL |
| ---- | 4/19 | ---- | 4/19 |
| 5/13 | ---- | 5/13 | ---- |
| ---- | 5/26 | ---- | 5/26 |
| 6/07 | ---- | 6/07 | ---- |
| ---- | 6/22 | ---- | 6/22 |
| 7/06 | ---- | 7/06 | ---- |
| ---- | 7/18 | ---- | 7/18 |
| 8/01 | ---- | 8/01 | ---- |
| ---- | 8/16 | ---- | 8/16 |
| 9/06 | ---- | 9/06 | ---- |
| 10/4 | 10/4 | 10/4 | 10/4 |
| ---- | ---- | 11/3 | 11/3 |
| 6 | 6 | 7 | 7 |
| TOTAL NUMBER OF HARVESTS | | | |
| 1989 | | | |
| ---- | 4/25 | ---- | 4/25 |
| 5/8 | ---- | 5/8 | ---- |

Table 10. Study termination plant density measurements averaged for all cultivars and harvest treatments for the Perkins Experiment.

| | CULTIVAR | | | | |
|---|---|---|---|---|---|
| | Adv | WL-320 | Baron | 5929 | Mean |
| TREATMENT | plants/$m^2$ | | | | |
| Control | 145.0 | 168.0 | 80.0 | 36.7 | 107.5 |
| Spring | 150.0 | 130.7 | 76.7 | 25.7 | 95.0 |
| Fall | 163.0 | 173.3 | 90.7 | 23.3 | 112.0 |
| Spring/Fall | 139.7 | 157.3 | 97.7 | 22.0 | 104.0 |
| Mean | 149.4 | 157.3 | 86.3 | 26.9 | |

Harvest Means LSD(0.08) = 13.1

Cultivar Means LSD(0.05) = 14.1

Cult. within Trt. LSD(0.05) = 16.7

# CHAPTER III

## CULTIVAR AND TEMPERATURE EFFECTS ON ALFALFA CARBON DIOXIDE EXCHANGE RATES

## ABSTRACT

Several researchers have reported an absence of total nonstructural carbohydrate (TNC) differences in alfalfa (Medicago sativa L.) roots during fall harvest management studies. A combination of available photosynthetic material and favorable environmental conditions may be responsible for maintaining TNC concentrations during the late fall and winter in the southern states. Rate of $CO_2$ assimilation during periods of adverse growing conditions may also be a factor determining long-term persistence and health of an alfalfa stand. Even though many photosynthetic studies have been conducted on alfalfa, there is still some controversy on the differential response to temperature. Research in this area has been largely confined to plant responses to optimum and high temperatures. no studies have reported on the photosynthetic response of alfalfa to fall growing conditions, especially the climatic conditions typical of the southern Great Plains environment. The purpose of this experiment was to determine the photosynthetic response of alfalfa genotypes previously selected for varying dormancy levels to

temperatures typical of environmental conditions prevalent during winter months in Oklahoma.

Four replications of four genotypes ('Advantage', 'WL-320', 'Baron', and 'Pioneer 5929') were acclimated in a growth chamber for five days to 20/10, 10/5, and 5/5 C day/night temperatures in 14, 12, and 10-hour photosynthetic periods, respectively, prior to measurement. The carbon dioxide exchange rates (CER) of the topmost fully expanded leaves were measured at each decending temperature regime. Plants were subjected to cell freezing temperatures (-10 C for four hours) and subsequently allowed to regrow for twelve days to twenty cm height. The CER was again measured after acclimation to ascending day/night temperatures (5/5, 10/5, and 20/10 C). Photosynthetic photon flux density was supplied by fluorescent and incandescent lamps at 640 mmol $m^{-2}$ $sec^{-1}$ at the tops of pots. Carbon dioxide exchange rates were measured with a Li-Cor (Li-Cor Inc., Lincoln, NE) $CO_2$ analyzer on attached leaves and expressed on a per unit leaf area basis (umol $m^{-2}$ $s^{-1}$). Moisture, nutrient and insect stress was minimized in the controlled environment of the growth chamber.

Alfalfa genotypes selected for high and low dormancy levels did not significantly differ in CER within any given temperature regime. Both CER and stomatal conductance ($G_s$) values decreased with decreasing temperatures,especially between 10 and 5 C, prior to cell freezing temperature exposure. After freezing, $G_s$ was higher than before freezing, while CER increased steadily with increasing temperatures and was higher at 5 C but lower at 10 and 20 C than prior to freezing.

Thus, CER and $G_s$ showed a high correlation prior to freezing, but were not correlated after freezing. Apparently, specific rate-limiting enzymes may have a depressed regeneration capacity after regrowth of leaf tissue following cell freezing temperatures.

# INTRODUCTION

Carlson et al. (1970) suggested that differences in photosynthetic rates in alfalfa (Medicago sativa L.) were heritable and increased yields could be obtained by selection for increased photosynthetic potential. Yoshida (1972) postulated that leaf area and photosynthetic rate directly influence dry matter production, which was confirmed by Delaney and Dobrenz (1974). Leaf temperature, light, carbon dioxide concentration, plant water status and water vapor gradient are factors that directly affect the rate of photosynthesis (Coyne and Bradford, 1984). The cultivar with the best adaptability to environmental factors must also be highly plastic in photosynthetic responses (Mooney and West, 1964; Mooney and Harrison, 1969; Pearson and Hunt, 1972).

Photosynthesis is an enzyme mediated process, therefore, it is temperature dependent. Low temperatures may inhibit photosynthesis by directly affecting enzymatic activity and decreasing $CO_2$ diffusion rates. Woldge and Dennis (1982), studying white clover leaves, reported an increased photosynthetic rate from 5 to 18 C. Few studies have reported on low temperature photosynthetic response of alfalfa.

The optimum temperature range for photosynthesis depends on the plant species. Plants which fix $CO_2$ by the malate pathway ($C_4$ plants) generally have a higher temperature optima for net $CO_2$ assimilation rate than plants that fix $CO_2$ only by the Calvin cycle ($C_3$ plants) (Berry and Bjorkman, 1980). Warm season $C_4$ species are photosynthetically more efficient than cool season $C_3$ species at their respective optimum

temperatures for photosynthesis because they possess a mechanism and anatomy for increasing the concentration of $CO_2$ available for the Calvin cycle, which is localized in the bundle sheath cells of $C_4$ species (Salisbury and Ross, 1978). Oxygen also competes with $CO_2$ for the ribulose bis-phosphate (RuBP) carboxylase:oxygenase enzyme, so an increase of $CO_2$ in the bundle sheath cells of $C_4$ plants reduces the reaction of RuBP carboxylase:oxygenase with $O_2$ resulting in little photorespiration (Hall and Rao, 1988). The mesophyll cells of $C_4$ plants fix $CO_2$ into 4-carbon acid compounds with the help of the enzyme phosphoenol pyruvate (PEP) carboxylase. The 4-carbon acids are transferred to bundle sheath cells, decarboxylated, and the resulting $CO_2$ is then refixed by the enzyme (RuBP) carboxylase in the Calvin cycle (Hall and Rao, 1988). One of the advantages of the $C_4$ system is that a small amount of $CO_2$ released from photorespiration in the bundle sheath cells is refixed by PEP carboxylase in the cytoplasm of the outer mesophyll cells (Hall and Rao, 1988). Consequently, an increase in the $CO_2$ concentration in the bundle sheath cells of $C_4$ plants would increase the net $CO_2$ fixation rate.

The photosynthetic response of leaves to temperature is sensitive to light intensity. Under rate-saturation light intensities, $C_4$ plants have a greater photosynthetic response to temperature than $C_3$ plants (Nobel, 1983). Net photosynthesis in single leaves of $C_4$ species is saturated only at photon flux densities above full sunlight (>2,000 mmol quanta $m^{-2}s^{-1}$) (Nobel, 1983), while in $C_3$ species it is saturated at photon flux densities one-quarter of full sunlight, or less (Clifford 1974). As light intensity is lowered, the temperature response curve

becomes flatter and broader (Coyne and Bradford, 1984). At low temperatures, the light intensities required to saturate photosynthesis are lower than at high temperatures, and if light intensity is reduced temperature has little effect on photosynthesis until the light intensity becomes limiting at that temperature (Berry and Bjorkman 1980). Woldge and Dennis (1982) found a rise in photosynthesis in bright light as temperature increased to the optimum, which was mainly attributed to a fall in the residual resistance consisting of mesophyll plus carboxylation plus excitation resistances. However, there was also a small decrease in stomatal resistance with increased temperature, and this was associated with a decrease in the internal substomatal $CO_2$ concentration ($C_i$).

Even though many photosynthetic studies have been conducted on alfalfa, there is still some controversy on the differential response to temperature. Research in this area has been largely confined to cultivars responding to optimum and high temperatures. Brown and Radcliffe (1986) found that the optimum temperature for apparent photosynthesis in stem tips was between 25 to 30 C. Furthermore, Pearson and Hunt (1972) measured the effect of temperatures on net carbon dioxide intake of whole alfalfa shoots. The temperatures ranged from 10 to 40 C in 10 C increments. They observed a steep decline in net $CO_2$ intake with increasing temperature (20 mg $dm^{-2}h^{-1}$ at 10 C to 5 mg $dm^{-2}h^{-1}$ at 40 C), for plants grown at 20/15 C day/night temperatures. In contrast, a less rapid decline was recorded by Murata et al. (1965) when they measured a wide range of temperatures, (from 5 to 30 C), for

apparent photosynthesis in whole alfalfa seedlings. The net $CO_2$ intake decreased from 25 mg $dm^{-2}h^{-1}$ at 10 C to 15 mg $dm^{-2}h^{-1}$ at 40 C.

In the southern states, several assumptions have been made about the effects of winter temperatures on photosynthesis and photosynthate partitioning in alfalfa. Sholar et al. (1983) in Oklahoma, Reynolds (1971) in Tennessee, and Mays and Evans (1973) in Alabama, independently suggested that mild daily maximum temperatures in winter months and the presence of green leaves on alfalfa plants might allow some photosynthetic activity, which could result in adding carbohydrate to the total root reserve. Edmiston and Wolf (1988) noted that slow regrowth, low respiration rates and relatively high photosynthetic rates resulting from cool temperatures limited TNC losses following fall harvests in Virginia. A favorable environment during fall regrowth results in the presentation of greater available leaf area for considerable photosynthesis to occur after fall harvest. Since the prostrate fall growth habit presents low demand for photosynthate for new foliar tissue, this should enhance the plant's capability to recharge root reserves. Thus, a critical carbohydrate recharge period prior to the first killing freeze may be less important in southern latitudes than in the north.

The objective of this study was to describe the effects of sub-optimal temperature on carbon dioxide exchange of alfalfa and compare the gas exchange characteristics of alfalfa cultivars with differing dormancy related growth patterns.

# MATERIALS AND METHODS

Four cultivars of alfalfa (Advantage, WL-320, Baron, and Pioneer 5929) were selected for a range of dormancy levels from high to low, respectively. Seeds were sown in 20-cm pots containing a 1:4 (by volume) mixture of peat:sandy loam soil then thinned to two plants/pot. Plants were watered regularly, fertilized once a week with Hoagland's Solution, monitored daily for insects which were controlled with a systemic insecticide when necessary, and clipped to five cm height at the recommended 10% bloom stage of growth to simulate ideal growing conditions. The plants were divided into two groups dependent upon plant age for experimentation. One group of plants with four replications was grown through twelve complete growth/harvest cycles while another complete group was grown through six cycles prior to the experiment. These two groups were considered separate plant age treatments in the experiment. Plants were introduced to a growth chamber environment two harvest/growth cycles prior to starting measurements.

All $CO_2$ exchange rate (CER) measurements were made using a stirred, temperature and humidity controlled reaction chamber (cuvette) described by Coyne and Bradford (1984). Humidity was measured in the cuvette with a condensation dew-point hygrometer (1111D General Eastern, Watertown, MA) and $CO_2$ was monitored by diverting the chamber exhaust through the sample cell of a portable infrared gas analyzer (LI-6200, Li-Cor Inc., Lincoln, NE). Measurements were made on the topmost fully developed,

intact trifoliolate leaf, using one leaf from each plant for each cultivar per replication. Photosynthetic photon flux density (PPFD) was measured with a quantum sensor (Li-190SB, Li-Cor Inc., Lincoln, NE). Cuvette conditions (leaf temperature, $CO_2$ concentration and dew point) were monitored using a computer-interfaced data acquistion system. After CER measurements were taken, leaf area was determined using an area meter (LI-3000, Li-Cor Inc., Lincoln, NE).

Upon first introduction to the growth chamber, plants were acclimated to a 20/10 C (day/night) temperature range and 14 hour photoperiod for two harvest/growth cycles. Photosynthetic photon flux density was supplied by fluorescent and incandescent lamps at 640 mmol quanta$^{-1}$ m$^{-2}$ sec$^{-1}$ at the tops of the pots. The $CO_2$ exchange rate was measured at 20, 10, 5 C following a four to five day acclimation interval at each of three temperature regimes (20/10 C, 10/5 C, 5/5 C), respectively. Photoperiod duration was 14 hours (20/10 C), 12 hours (10/5 C), and 10 hours (5/5 C) during the respective acclimation intervals. Plants were then subjected to cell freezing temperatures (-10 C for four hours) and allowed to regrow to 10 cm at 20/10 C. The $CO_2$ exchange rate was again measured after regrowth periods of 5/5 C, 10/5 C, and 20/10 C with a four to five day acclimation interval. The three temperature regimes for which CER was measured prior to subjecting plants to cell freezing temperatures will be referred to as prefreeze. The three regimes for which CER was measured after freezing temperatures were applied will be referred to as postfreeze. Measurements from the resulting six temperature treatments (3 prefreeze and three postfreeze)

were each analyzed separately with a completely randomized design with four replications of each cultivar for each plant age.

# RESULTS

Alfalfa genotypes selected for high and low dormancy levels did not differ significantly in CER (umol $m^{-2}s^{-1}$) within any given temperature regime (Figures 1 and 2). The range in CER response among all cultivars was less at the 5 C temperature than at the higher temperatures for both prefreeze and postfreeze measurements. The maximum observed values for CER were 13.7 umol $m^{-2}s^{-1}$ prefreeze and 9.3 umol $m^{-2}s^{-1}$ in postfreeze at 20 C.

Averaged across all cultivars, CER were significantly different between prefreeze and postfreeze at the 5% level for all temperature regimes (figure 5). Postfreeze CER was significantly greater ($P \leq 0.05$) at 5 C than prefreeze. However, the reverse was true at 10 C and 20 C. The CER response at 5 C postfreezing was greater than twice the prefreeze rate, while at 10 C and 20 C the prefreeze CER was nearly double the postfreeze rate.

Prior to freezing, when temperatures were decreased from 20 C to 10 C, there was very little change in CER. However, the level of CER was significantly depressed as temperatures were decreased from 10 C to 5 C for all cultivars. In constast, there was no significant difference ($P \leq 0.05$) as temperatures increased from 5 C to 10 C postfreeze, and only a slight increase at 20 C. (Figure 5).

Cultivars did not differ significantly in stomatal conductance $G_s$ within any temperature regime (Figures 3 and 4) although they ranged considerably. Prefreeze $G_s$ decreased significantly from 10 C to 5 C,

after remaining static between 20 C and 10 C (Figure 3). Averaged across all four cultivars, $G_s$ decreased from a high of 0.29 mol $m^{-2}s^{-1}$ at 20 C to a low of 0.14 mol $m^{-2}s^{-1}$ at 5 C prefreeze (Figure 6). Postfreeze the $G_s$ averaged across all four cultivars increased from a low of 0.36 mol $m^{-2}s^{-1}$ at 5 C to a high of 0.47 mol $m^{-2}s^{-1}$ at 10 C (Figure 6). Postfreeze $G_s$ was significantly greater than prefreeze $G_s$ at the 5% level for all temperature regimes (figure 6).

# DISCUSSION

Data support the hypothesis that a reduction of CER results from thermal stress. Sub-optimal temperatures apparently caused an adverse affect on biochemical reactions of the photosynthetic apparatus. Fitter and Hay (1981) have indicated that in $C_4$ plants a reduction in CER at sub-optimal temperatures was due to a reduced capacity of specific rate-limiting enzymes, such as phosphoenol (PEP) carboxylase and ribulose-bisphosphate (RuBP) carboxylase. As temperature changes from the optima for CER, the activation of these two enzymes also decreases. This decrease in enzyme activity for fixing $CO_2$ could result in an increased resistance to carbon dioxide transport between the internal substomatal air spaces and the chloroplasts in the mesophyll cells (Coyne et al. 1982).

Chatterton and Carlson (1980) found that the relatively large yield differences among alfalfa plants grown under field conditions are minimized under controlled environments where root nodulation is prevented by nitrogen fertilization and moisture and nutrient stresses are minimized. Data collected by Chatterton and Carlson (1980) show a higher CER value in leaves of 10-hour than 14-hour photosynthetic grown plants. These higher values are thought to be an expression of acclimation of CER to photosynthetic period (Chatterton and Silvius, 1979). An apparent absence of rapid acclimation was noted when alfalfa plants were shifted from a long to a short daily photosynthetic period for four days (Chatterton and Silvius, 1980). A similar effect was also

noticed in these results, since after cell freezing temperatures were administered, the alfalfa cultivars did not increase CER in response to increasing photosynthetic period or temperature to the same level as measured after exposure to similar temperature/photoperiod regimes prior to freezing.

Wong et al. (1985) observed that CER and leaf conductance ($G_s$) in plants of maize (Zea mays L.) were linearly related at constant temperature with varying ambient $CO_2$ concentration, irradiance and mineral nutrition. In the present study, both CER and $G_s$ decreased as measurement temperature decreased prior to freezing. These results would indicate that stomata close with sub-optimal temperatures. However, postfreeze CER and $G_s$ did not respond linearly in response to increasing temperatures (Figure 7). Furthermore, $G_s$ was much higher post freezing than prior to freezing (Figure 6), while CER was higher at 5 C but lower at 10 and 20 C (Figure 5). These results contrast with previous studies which indicate that stomata open in response to increasing temperatures (Crookston et al., 1974; and Drake et al., 1970). Since CER and $G_s$ were linearly related prior to cell freezing temperatures, but not afterwards, and since Cer showed very little temperature response after freezing, the results suggest a possible deficiency of RuBP carboxylase regeneration potential by the plant (Fitter and Hay, 1981; and Caemmerer and Farquhar, 1984).

Stomatal conductance prior to freezing appeared to affect CER in this study. Stomatal conductance appeared to have a prominent role in determining CER below an optimum temperature. These results correspond

with a previous study in corn showing a decrease in $G_s$ and CER at sub-optimal temperatures (Raschke, 1970). Raschke (1970) reported that at temperatures around 10 C, net uptake of $CO_2$ amounted to only 20 to 30% of that measured at 30 C, the optimum temperature for net $CO_2$ uptake in corn. The loss of stomatal conductance at low temperatures may be advantageous as it increases the leaf temperature above air temperature (Linacre, 1964). However, in this study, $G_s$ of alfalfa after freezing was not correlated with CER. After plants recovered from freezing, $G_s$ was high at all temperatures, however, CER was low, further supporting the premise that enzymatic activity was depressed. It appears the increased flux of $CO_2$ into the stomatal aperture could not compensate for the decreased ability to fix $CO_2$, due to the apparent inactivity of RuBP carboxylase. Other studies (Raschke 1970) have also shown a lack of correlation of $G_s$ and CER at high temperatures.

# SUMMARY AND CONCLUSIONS

Some basic information on photosynthetic characteristics of alfalfa at sub-optimal temperatures was collected for the first time. The four cultivars studied, though adapted for forage and seed production in different environments, were not different in their photosynthetic response to temperature. The CER achieved at the most optimum temperature studied (20 C) was 13.7 umol $m^{-2}$ $s^{-1}$ prior to freezing, and 9.3 umol $m^{-2}s^{-1}$ for regrowth after freezing. Carbon dioxide exchange rate differed little between 20 and 10 C, but decreased dramatically with decreasing temperatures from 10 C to 5 C prior to freezing. After freezing, CER recovered quickly at 5 C, then increased steadily with increasing temperature. Stomatal conductance also showed a large decrease as measurement temperatures decreased from 10 C to 5 C prior to freezing; but after freezing $G_s$ was considerably higher and showed less response to temperature. Carbon dioxide exchange rate and $G_s$ showed a high correlation in prior to freezing; but after freezing, showed no correlation. Thus, specific rate-limiting enzymes may have a depressed regeneration capacity after regrowth of leaf area following exposure to cell freezing temperatures.

Further studies should be done in order to conclusively investigate alfalfa's photosythetic response to low temperatures. No studies have yet been conducted on alfalfa's photosynthetic response to illuminance, moisture stress and nutrition at sub-optimal temperatures. Further investigations of varietal differences is not suggested, as the broad

range of cultivars with differing dormancy characteristics evaluated in this study were found to react in a similar photosynthetic manner when studied in a controlled chamber.

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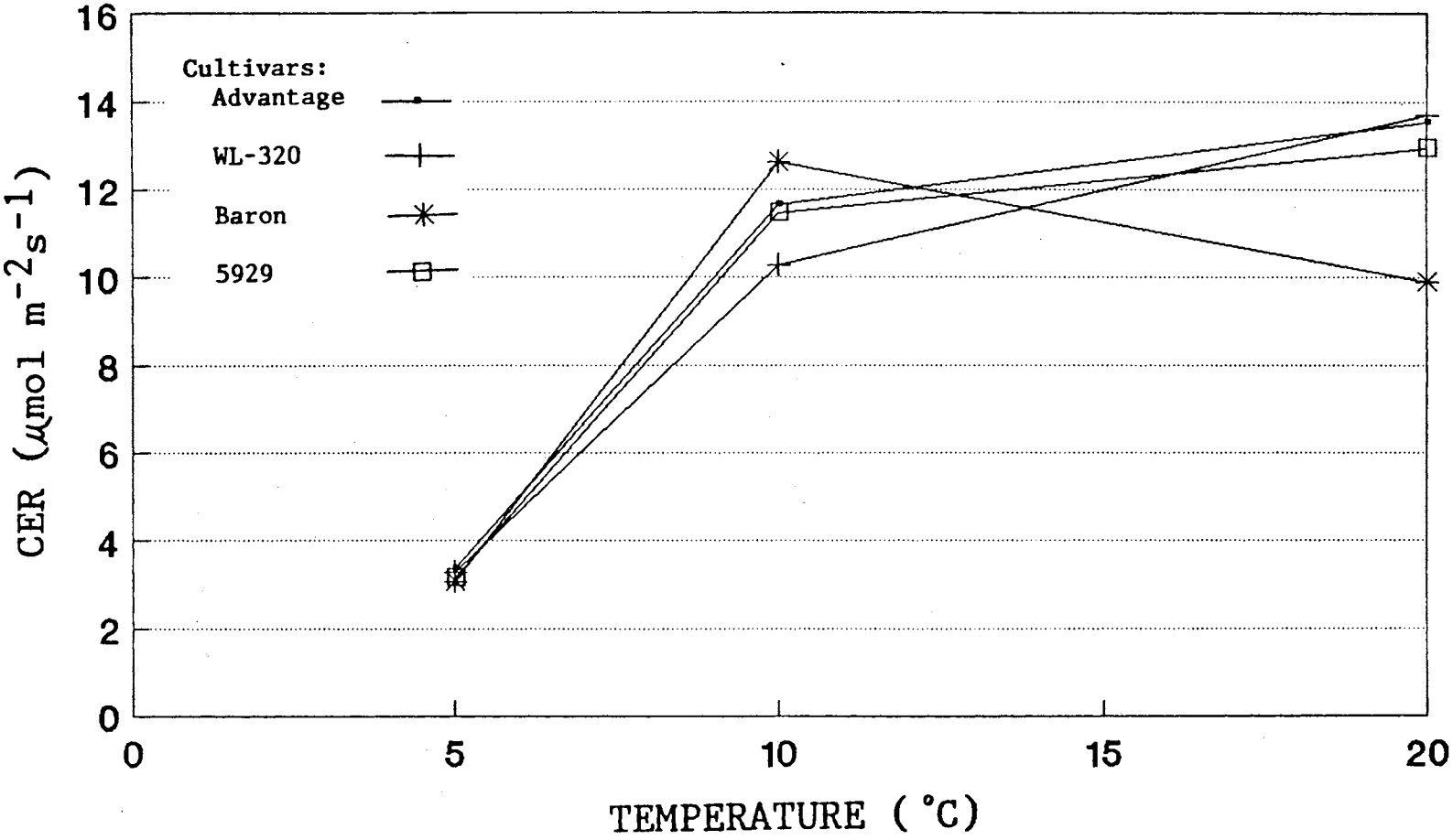


Figure 1. Response of $CO_2$ exchange rate (CER) to leaf temperature prior to application of cell freezing temperatures for four cultivars.

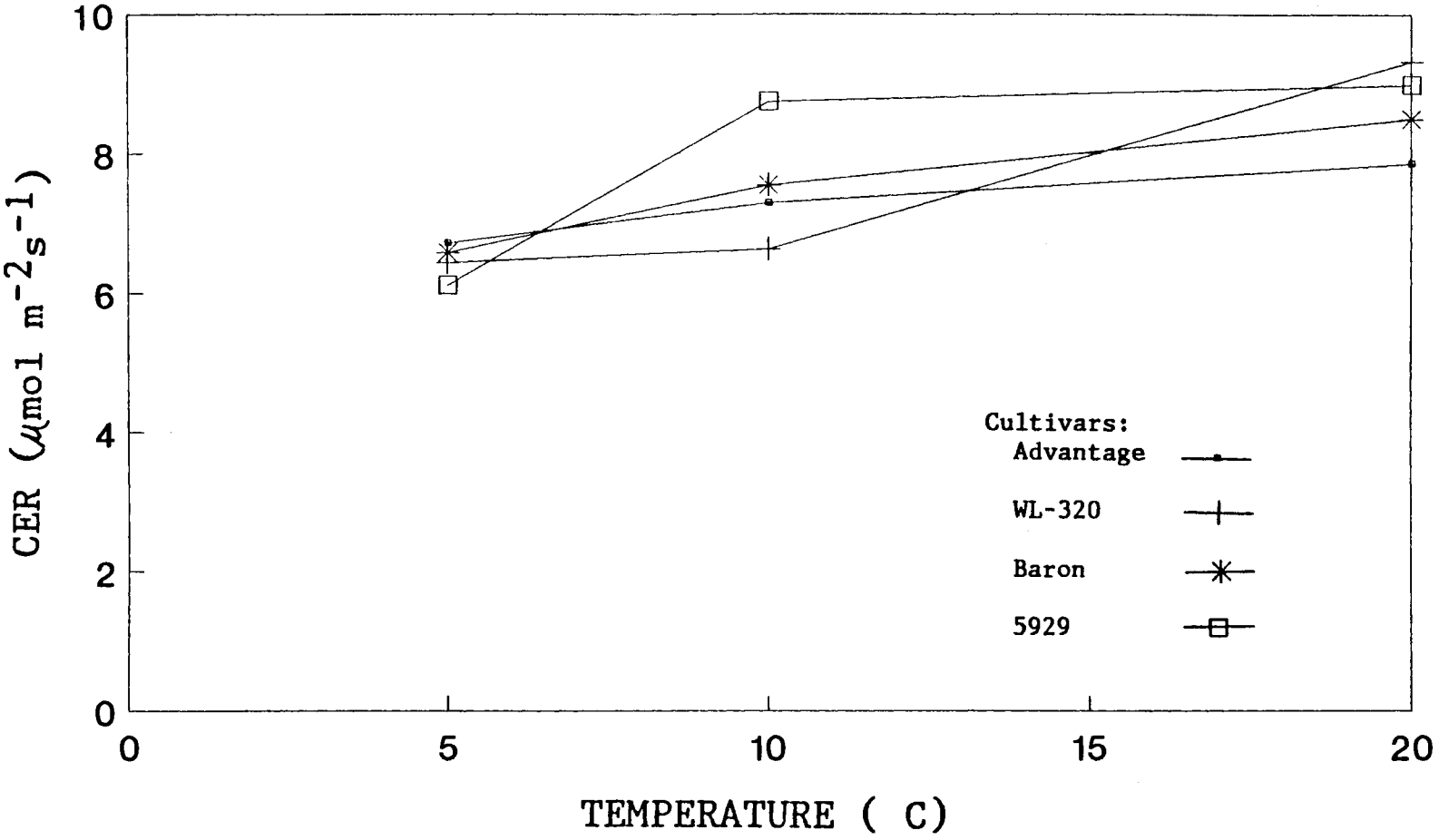


Figure 2. Response of $CO_2$ exchange rate (CER) to leaf temperature after freezing temperatures were applied for four cultivars.

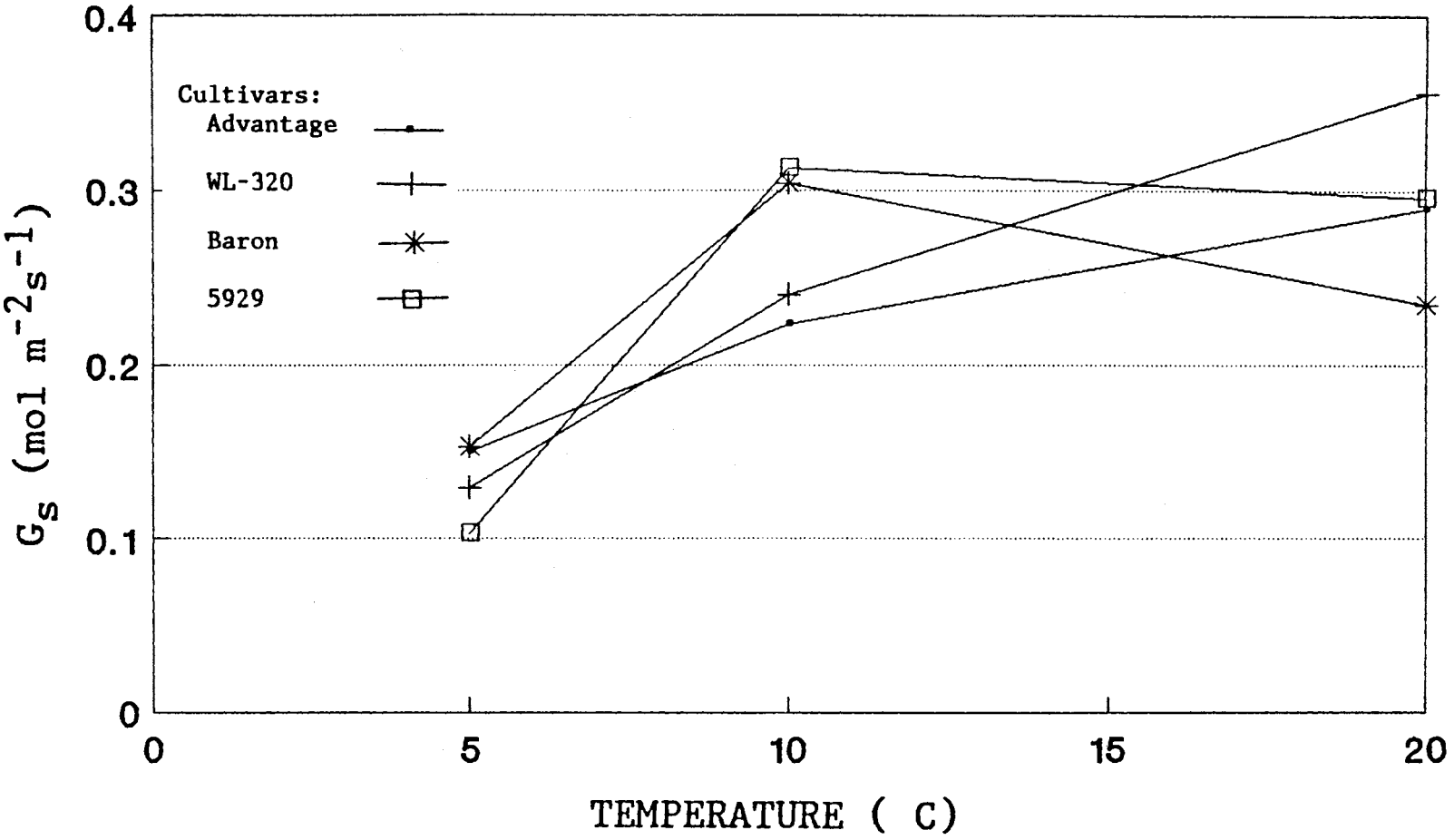


Figure 3. Response of stomatal conductance ($G_s$) to leaf temperature prior to application of cell freezing temperatures for four cultivars.

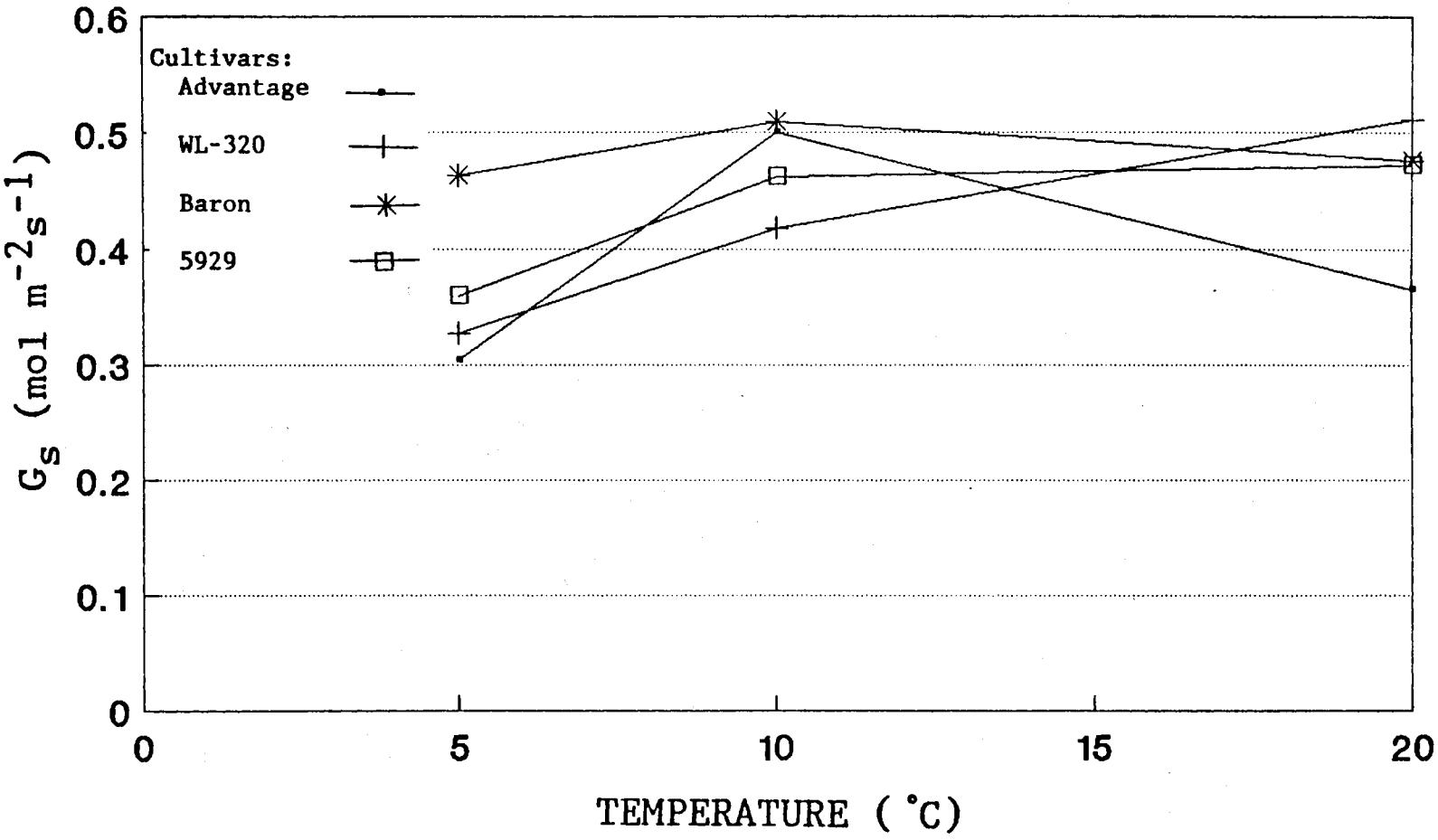


Figure 4. Response of stomatal conductance ($G_s$) to leaf temperature after application of cell freezing temperatures for four cultivars.

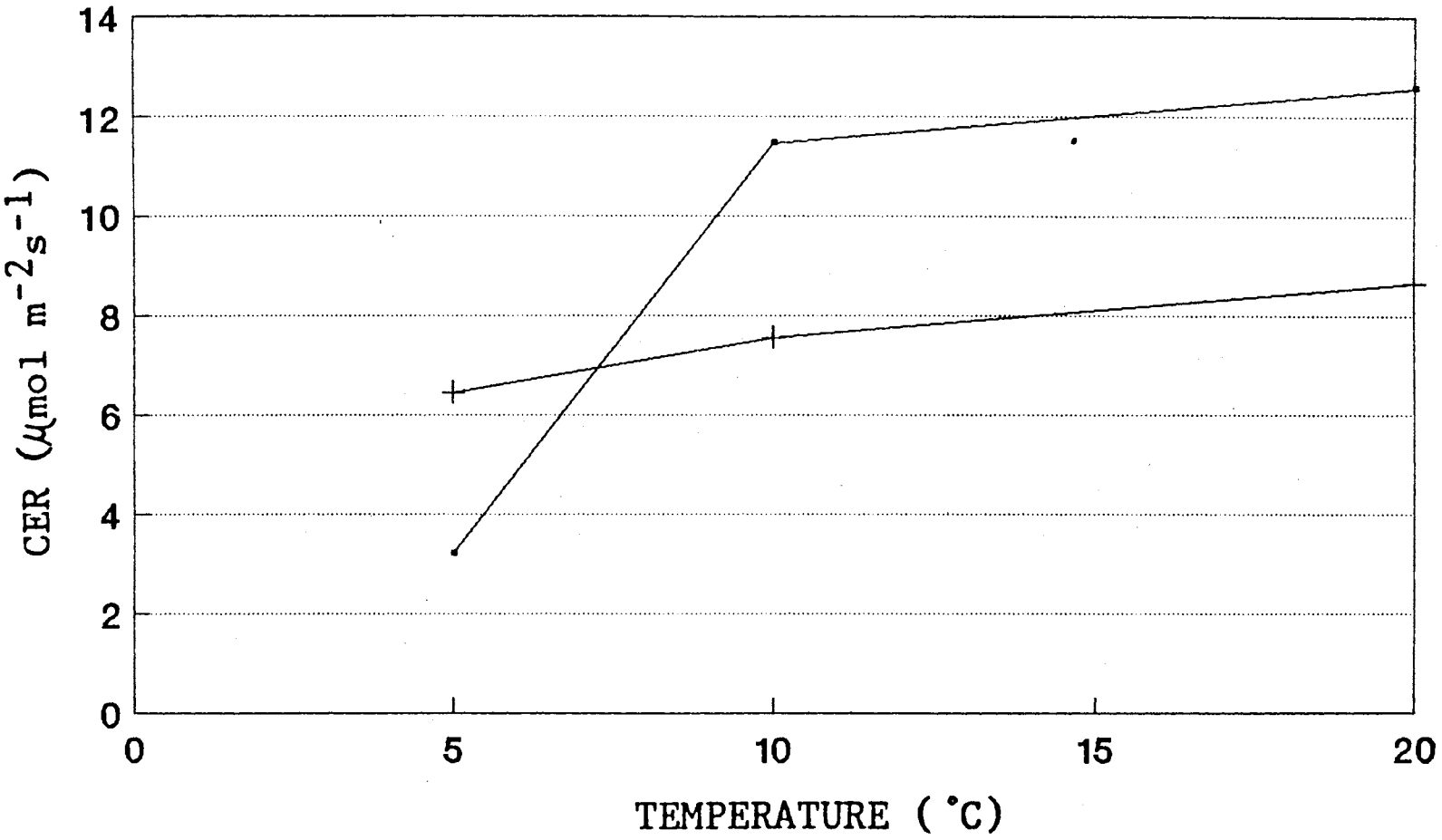


Figure 5. Comparison of $CO_2$ exchange rate (CER) to leaf temperatures averaged across all cultivars prior to ( —•— ) and after cell freezing temperatures ( —+— ).

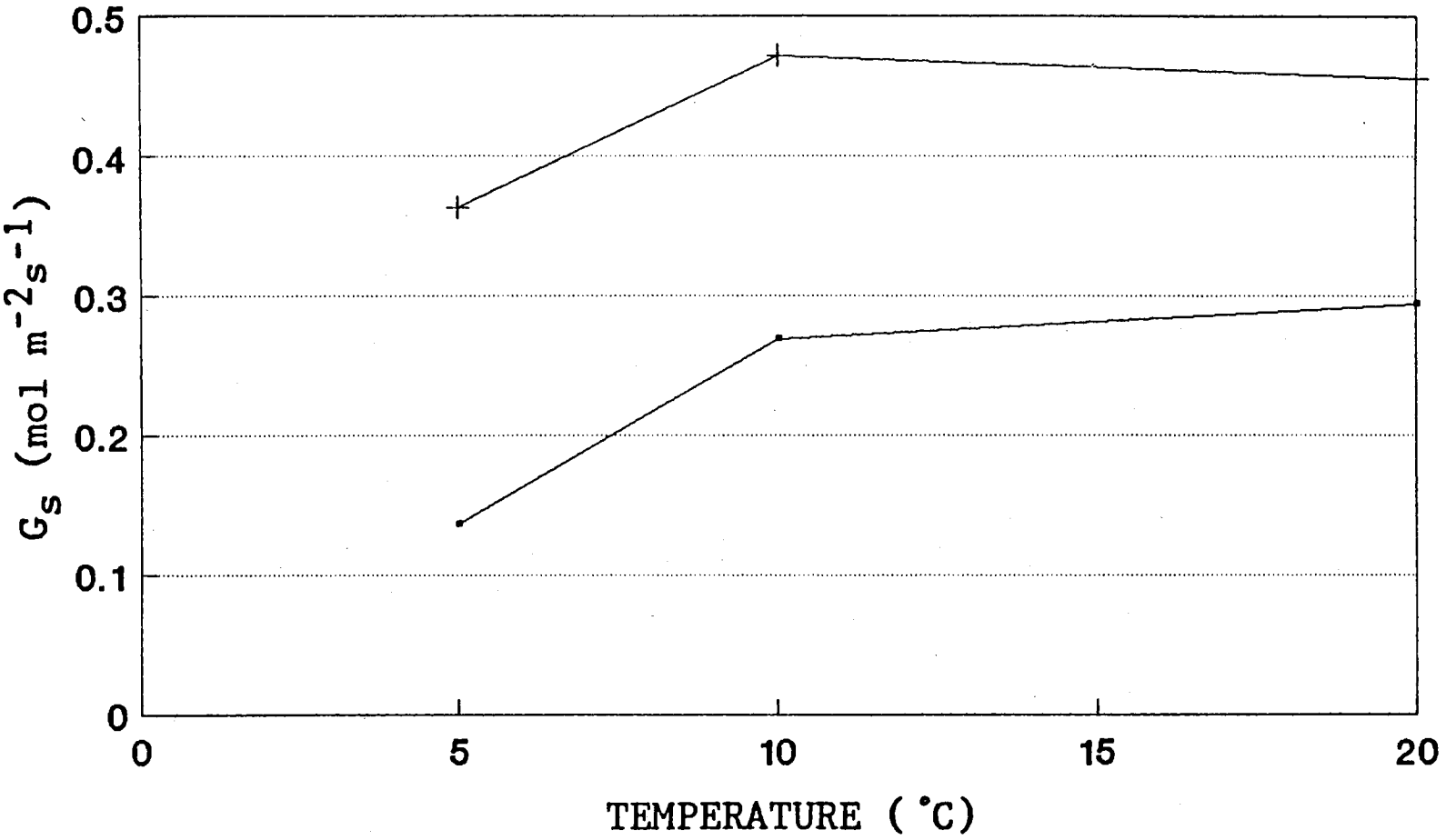


Figure 6. Response of stomatal conductance ($G_s$) to leaf temperature averaged across all cultivars prior to ( —•— ) and after cell freezing temperatures( —+— ).

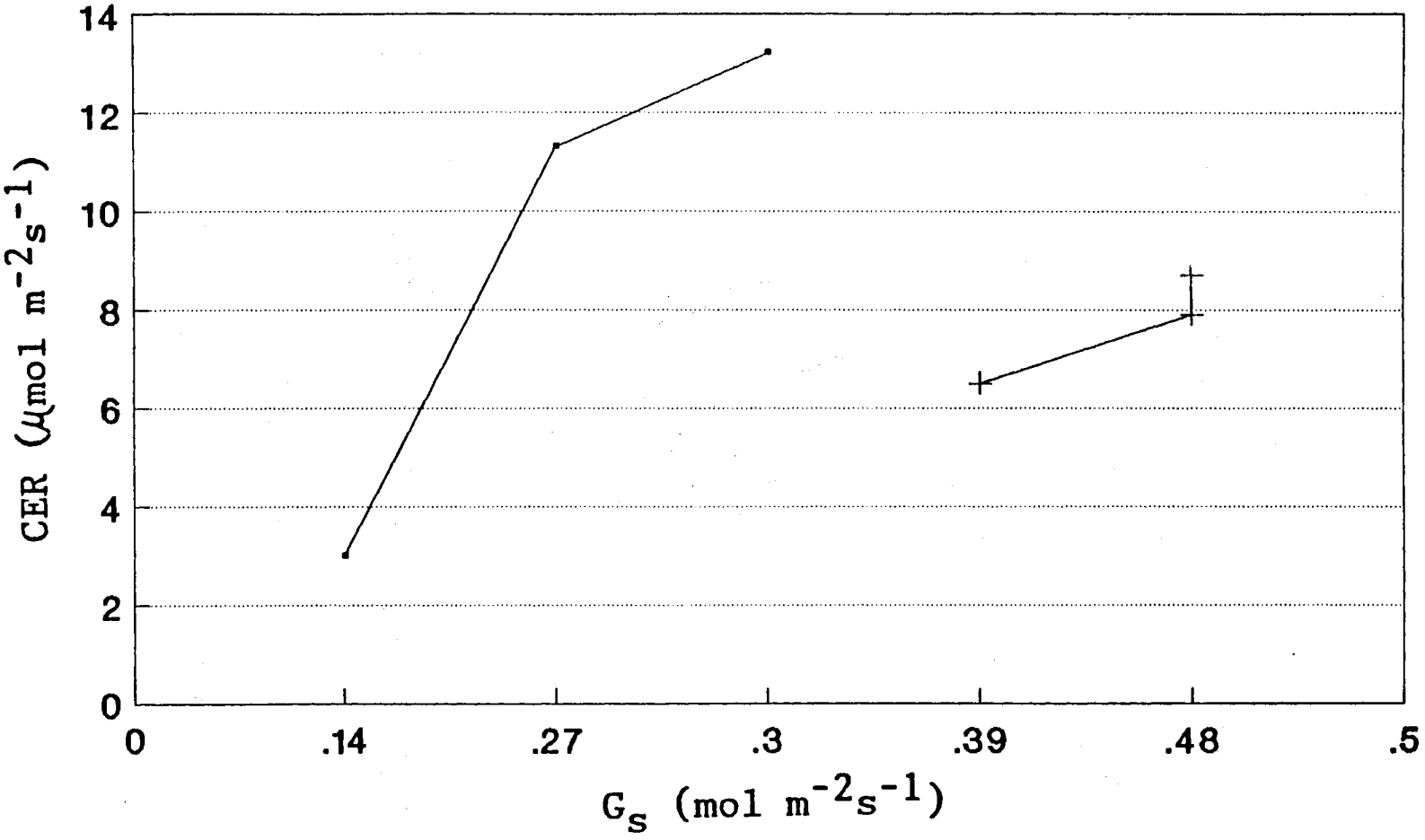


Figure 7. A comparison of mean carbon dioxide exchange rates and (CER) stomatal conductance ($G_s$) prior to ( —•— ) and after cell freezing temperatures ( —|— ).

VITA

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