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The Importance of Carbon Balance and Root Activity in Creeping Bentgrass Tolerance to Summer Stresses

Submitted by

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EXECUTIVE SUMMARY

It was proposed that imbalanced photosynthesis and respiration process and carbohydrate depletion could be the primary physiological factors contributing to bentgrass quality decline under high temperature and close mowing conditions. The overall objective of the project was to test this hypothesis in creeping bentgrass cultivars grown under close mowing and high temperature stresses. This project involved two studies, in which responses of turf quality, root growth, viability, and carbohydrate metabolic activities for four creeping bentgrass cultivars to high temperatures and close mowing conditions were examined in controlled environment growth chambers.

The first study investigated effects of differential shoot/root temperatures and mowing frequency on turf and root growth and carbohydrate metabolic activities to determine whether turf quality and carbon balance could be improved by modifying root temperatures. In this study, two widely grown bentgrass cultivars, Crenshaw and Penncross, and two relatively new cultivars with promising summer performance under close mowing, L-93 and Penn A-4, were examined. Grasses were exposed to differential shoot/root temperatures, including low shoot/root (20/20 C; control), low shoot/high root (20/35 C), high shoot/low root (35/20 C), or high shoot/root (35/35 C) conditions. Grasses were mowed at a 3-4 mm height daily or on alternate days. It was found that turf quality and root activity were much lower at high root (20/35) or high shoot/root (35/35 C) temperatures than those of their respective controls for all four cultivars. Reducing root temperature to 20 C while maintaining shoots at 35 C improved turf quality and root growth to levels similar to those of the control treatment. High shoot/root temperatures reduced canopy photosynthetic rate caused imbalance between photosynthesis and respiration and carbon deficit, whereas reducing root temperatures reversed, to some extent, the adverse effects of high shoot/root temperature on carbon balance. The decline in turf quality was more severe for Penncross than Crenshaw, L-93 and Penn A-4 under high root or shoot/root temperatures. Similarly, daily carbon consumption to production ratio was higher for Penncross than other cultivars under high root or shoot/root temperatures when grasses were closely mowed daily. Extending mowing frequency from daily to every other day improved turf quality and root growth, especially under high root or shoot/root temperatures, which was accompanied by enhanced photosynthetic rate and reduced carbon consumption to production ratio.

The second study examined whether declines in shoot and root growth with increasing temperatures (20, 24, 30, 34, and 38 C)

were related to changes in carbohydrate metabolisms in Penncross under close mowing conditions. Turf quality, root growth and viability of Pencross declined significantly with increasing temperature to 30 C and higher. The imbalance between photosynthesis and respiration, carbon deficit, and reduced carbohydrate availability also occurred as temperatures exceeded 30 C.

Results from both studies clearly demonstrated that: 1) Carbohydrate depletion was a major physiological cause of summer bentgrass decline under high temperatures and close mowing. This was related to the imbalance between photosynthesis and respiration, which was caused by severe decline in photosynthesis capacity under high temperatures and low mowing; and 2) Roots played important roles in the regulation of creeping bentgrass tolerance to high temperature stress. Therefore, reducing root-zone temperature improved turf quality.

Two manuscripts describing the results of the project are currently being prepared for submission to Crop Science by the end of 1998.

I. BACKGROUND

Creeping bentgrass (<u>Agrostis palustris</u>) is the most widely used cool-season turfgrass on golf greens. Loss of bentgrass is observed on most golf courses nearly every year in the transition and warm climate regions during summer months when greens receive maximum use (Lucas, 1995; Carrow, 1996). Pavur (1993) reported that some courses have lost a majority of bentgrass to the decline syndrome. Attempts to extend use of bentgrass into warmer climatic regions further accentuates the problem.

To date, it is not clear what physiological factors cause summer bentgrass decline. Understanding the cause of the decline problem will not only help to treat bentgrass decline, but also provide guidelines for developing cultural practices to prevent decline. Identification of physiological factors that could be incorporated into new germplasm through genetic breeding approaches to develop cultivars tolerant to close mowing and high temperatures will reduce the overhead costs for intensive management of bentgrass greens during summer.

Carbohydrate metabolism is a key process controlling plant growth, as it provides energy and carbon skeletons for plants (Hull, 1992). It is hypothesized that turf quality decline of creeping bentgrass grown under high temperature and close mowing conditions could result from carbohydrate starvation due to low photosynthetic rate (the process that produces carbohydrates) and high respiration rate (the process that consumes carbohydrates).

The overall objective of the project was to investigate the physiological causes of creeping bentgrass decline under close mowing and high temperature stresses.

II. MODIFICATION TO THE ORIGINAL PROPOSAL

In addition to the study originally proposed (Study One) on effects of root-zone temperature modification, we have conducted an additional growth chamber study (Study two), in which bentgrass responses to increasing temperatures were examined. This was done because we believe that information obtained would be important and pertinent to the objective and would strengthen the test for the proposed hypothesis.

III. OBJECTIVES

Study one: Root-zone temperature modification

1. To investigate whether shoot and root growth decline under high root, shoot or shoot/root temperatures and frequent, low mowing conditions could be related to carbohydrate metabolic activities.
2. To determine whether turf quality, root growth and carbon balance could be improved by modifying root-zone temperatures.

Study two: Bentgrass response to increasing temperatures

The objective of this study was to determine responses of turf quality, root growth and viability to increasing temperatures in relation to changes in carbohydrate metabolic activities.

IV. RESEARCH METHODOLOGY

Study one: Root-zone temperature modification

We examined Crenshaw and Penncross (grown widely on golf greens with contrasting heat tolerance), and Penn A-4 and L-93 (relatively new cultivars with promising performance under close mowing in the summer). L-93 was added in the study because was found in previous growth chamber and field studies that it exhibited good heat tolerance. Grasses were planted in a mixture of 10% profile and 90% sand in PVC tubes (20 cm dia. and 60 cm long) and watered daily with deionized water to field capacity.

To examine effects of differential shoot/root temperature on shoot and root growth, and carbohydrate metabolisms, four differential air/soil temperature regimes were imposed: a) 20/20 C; b) 35/20 C; c) 20/35 C; and d) 35/35 C. Root-zone temperature was controlled by maintaining the soil medium in water baths at 20 or 35 C. Air temperature at various distances from the canopy, canopy temperature, and root-zone temperature at different depths were measured with thermocouples connected to a thermometer. The temperature profiles from root zone to ambient air under the four temperature regimes are presented in Fig. 1.

Turf was mowed at a 3-4 mm height with an electric hair clipper in two different mowing frequencies: a) daily; and b) every other day.

At various times during the study, several shoot physiological parameters were measured on plants in four containers in each treatment. Leaf photochemical efficiency was measured with a chlorophyll fluorescence meter. Turf quality was visually rated. Canopy photosynthetic rate and dark respiration rate were measured with LiCor-6400 gas exchange system. Leaves were collected and kept frozen for the analysis of antioxidant enzyme activities.

At 17, 30, and 45 d after treatment, plants from four containers in each treatment were harvested. Leaves, crowns, and roots were oven-dried, and stored separately for carbohydrate analysis. Root viability was determined using TTC reduction method. Roots were stained with methyl violet and stored for root length and dry weight measurements.

Study two: Responses to increasing temperatures

Five-year-old sods of \`Penncross' were collected from the Rocky Ford Turfgrass Research Center, Manhattan, KS and established on a mixture of sand and fritted clay (Profile) (9:1, v/v). The soil medium was contained in polyvinyl chloride (PVC) tubes measuring 5-cm in diameter and 60-cm deep. Plants were maintained in a greenhouse for 60 d and then were transferred to growth chambers, with an average day/night temperature of 20/15 C, a PAR of 600 μmol m^{-2} s^{-1} at canopy level, and a 14-h photo period. Plants were mowed daily to a 3-4 mm height with an electric hair clipper. Turf was watered daily to prevent drought stress and fertilized weekly with half-strength Hoagland's solution (Hoagland and Arnon, 1950).

Plants were exposed sequentially to air temperatures of 20, 24, 30, 34, and 38 C. Plants were exposed to 20 C for 60 d and each of other temperature treatments for 20 d. Each treatment was repeated four times in four growth chambers.

At 60 d of 20 C and 20 d of 24, 30, 34, and 38 C treatment, various shoot and root parameters were determined. Turf quality was rated visually based on color, uniformity, and density on a 0 to 9 scale where 0 = worst quality, 6 or above = acceptable, and 9 = best quality. Canopy net photosynthetic rate (P_n) was measured from 10:00 to 14:00 h, and dark respiration rates of whole plant and soils were measured from 19:00 to 23:00 h with LI-6400 portable gas exchange system (LiCor Inc., Lincoln, NE). Respiration rate of whole plants (R_{plant}) including shoots and roots were determined by subtracting respiration rates of soils from that of both plants and soils. The P_n and R_{plant} were expressed as CO_2 uptake and evolution per unit turf canopy area, respectively. Daily carbon consumption to production ratio was calculated using the data of P_n and R_{plant} integrated over a 13-h photoperiod and 11-h dark period.

After the measurements described above, plants were harvested. Roots were separated from aboveground tissues and washed free of soil. Root dehydrogenase activity was measured with the TTC (triphenyltetrazolium chloride) reduction technique (Knievel, 1973). Root dry weight was measured after drying samples for 24 h at 85°C. Total nonstructural carbohydrate (TNC) content of shoots was measured using the method described in Smith et al. (1964).

RESULTS AND DISCUSSION

Study One: Root-zone temperature modification

Turf visual quality

Regardless of mowing frequency, turf quality for all four cultivars declined significantly when only root (20/35 C) or both shoots and roots (35/35 C) were exposed to high temperature (Fig. 2, 3, 4, and 5). Reducing root temperature to 20 C while shoot was maintained at 35 C improved turf quality when grasses were mowed daily or on alternate days. Turf grown at 35/20 C shoot/root temperature maintained quality similar to that at 20/20 C for all cultivars.

Turf quality was not affected by mowing frequency when grasses were grown under 20/20 C and 35/20 C temperature regimes for any of the four cultivars (Fig. 2, 3, 4, 5). However, grasses mowed on alternate days had better quality than those mowed daily when only root (20/35 C) or both shoots and roots (35/35 C) were exposed to high temperatures over 30 d (Fig. 6, 7). This was true for all four cultivars.

Among all cultivars, Penncross had the poorest quality under high root (20/35 C) or high shoot/root (35/35 C) temperatures when grasses were mowed daily or on alternate days.

Photochemical efficiency

Photochemical efficiency, expressed as chlorophyll fluorescence (Fv/Fm ratio), was reduced by high root (20/35 C) temperature or high shoot/root (35/35 C) temperature when grassed were mowed daily or on alternate days for all cultivars (Fig. 8, 9, 10, 11). The reduction in Fv/Fm at 20/35 C and 35/35 C shoot/root temperatures was more severe for Penncross than for Crenshaw, L-93, and Penn A-4. Reducing root temperature to 20 C improved photochemical efficiency in all cultivars.

Mowing frequency had no effect on Fv/Fm at 20/20 C and 35/20 C. Mowing on alternate days resulted in higher Fv/Fm ratio for all cultivars than when mowed daily after 30 d of high root or shoot/root temperature treatments (Fig. 12, 13).

Photochemical efficiency of Pencross and Crenshaw was lower than that of Penn A-4 and L-93 (when grasses were mowed daily) after 30 d of high root or high shoot/root temperatures (Fig. 12, 13). No cultivar variations in Fv/Fm were observed at 20/35 or 35/35 C when grasses were mowed on alternate days.

Root growth and activity

Root growth (Fig. 14) and activity (Fig. 15) were restricted by high root temperature (20/35 C) and high shoot/root temperature (35/35 C) when grasses were mowed daily or on alternate days for all four cultivars. Grasses grown under low shoot/root (20/20 C) or low root temperature (35/20 C) had larger root systems (Fig. 14) and greater root activity (Fig. 15) than those grown under high shoot/root (35/35 C) temperature conditions.

Grasses mowed on alternate days had bigger root systems than those mowed daily, especially under high root, shoot or shoot/root temperature regimes (Fig. 14).

Mowing had no effect on root activity for Penncross, Crenshaw, and Penn A-4, but mowing on alternate days increased root activity for L-93 under high root (20/35 C) and high shoot (35/20 C) temperature conditions (Fig. 15).

The reduction in root activity due to high root or shoot/root temperatures was less for L-93 than other three cultivars, compared to their respective controls (20/20 C), when grasses were mowed daily or on alternate days (Fig. 16). Compared among grasses mowed on alternate days at high root (20/35 C) or high shoot (35/20 C) temperatures, root activity of L-93 was higher than that of the other cultivars.

Photosynthesis and respiration rate

For all cultivars mowed daily or on alternate days, exposure to high root temperature (20/35 C), shoot temperature (35/20), or high shoot and root temperature (35/35 C) reduced canopy photosynthetic rate, compared to exposure to the low shoot and root temperature regime (20/20 C). However, the reduction in photosynthetic rate at 35/20 C and 20/35 C was much less dramatic than at 35/35 C (Fig. 17, 18). Under high root and shoot/root temperature conditions, grasses mowed on alternate days had higher photosynthetic rate than those mowed daily for all cultivars (Fig. 17).

Respiration rate was not affected as much as photosynthesis by differential temperatures. However, respiration rate (Fig. 19, 20) was higher than photosynthetic rate (Fig. 17, 18) under high shoot and root temperature (35/35 C) conditions. Under other temperature conditions, grasses maintained a respiration rate lower than or equal to photosynthesis rate. This pattern was true for all four cultivars.

In all cultivars examined, high shoot/root temperatures caused an imbalance between photosynthesis and respiration; whereas low shoot/root, root, or shoot temperature enhanced photosynthesis and improved the balance between the two carbon metabolic processes.

Daily carbon consumption and production

Carbon consumption to carbon production ratio was about 50% for grasses grown under low shoot/root temperature conditions in all cultivars when grasses were mowed daily or on alternate days for all cultivars (Fig. 21, 22, 23, 24). The ratio was higher at high root or shoot temperature than that at 20/20 C, but was still maintained around 1. However, under high shoot and root temperature conditions, carbon consumption to was about 2 to 10 times of carbon production, indicating that the amount of carbon consumed per day much exceeded that produced, which would lead to carbon starvation.

Under high shoot/root temperature conditions, Penncross (Fig. 21) had higher carbon consumption to production ratio than the other three cultivars (Fig. 22, 23, 24) when grasses were mowed daily.

Extending mowing to every other day reduced the carbon consumption to production ratio compared to daily mowing for all cultivars grown under high shoot, root or shoot/root temperatures. This indicates that taller turf had a more positive carbon balance than shorter turf.

Study Two: Responses to increasing temperatures

Turf visual quality and root growth

Turf quality (Fig. 25), root viability (Fig. 26A), and root dry weight (Fig. 26B) of Penncross declined as temperature increased to 30 C or higher. Turf quality declined to below an acceptable level at 34 and 38 C (Fig. 25). These results were consistent with our field observations in declines of turf quality and root growth in another study.

Photosynthesis and respiration rates

Similar to temperature responses of turf quality and root growth, net photosynthetic rate (P_n) of the canopy reduced significantly as temperature was elevated to 30 C or higher; P_n dropped to almost zero at 38 C (Fig. 27). Whole plant respiration rate (R_{plant}) increased as temperature increased from 20 C to 34 C, and then decreased at 38 C. Plant respiration rate exceeded P_n at 34 and 38 C. These results suggested that imbalance between photosynthesis and respiration process occurred as temperature increased to 34 C or higher.

Daily carbon consumption to production

Daily carbon consumed in the respiration process was about 58% of that produced in the photosynthesis process at 20 and 24 C (Fig. 28). The proportion of carbon consumption to production increased with temperatures. When temperature increased to 34 and 38 C, carbon consumption was about 2 to 4 times of carbon production. This result indicated that high temperature caused negative daily carbon gain, which could lead to carbon depletion as temperature increased.

Carbohydrate accumulation

Shoots exposed to 24 C had similar total nonstructural carbohydrate (TNC) content as those at 20 C (Fig. 29). However, carbohydrate availability in shoots decreased as temperature increased to 30 C or higher. Shoots grown at 30, 34 and 38 C had significantly lower TNC than those of their control plants grown at 20 C. This result suggested that carbohydrate availability decreased with temperatures, which could be due to the imbalance between photosynthesis and respiration as discussed above.

CONCLUSIONS

We have clearly demonstrated that:

1. ***Carbohydrate depletion was a major physiological cause of summer bentgrass decline under high temperature and close mowing conditions. This was related to the imbalance between photosynthesis and respiration, which was caused by a severe decline in photosynthesis activity under high temperatures and low mowing.***
2. ***Roots played important roles in the regulation of creeping bentgrass tolerance to high temperature stress.***

These conclusions were strongly supported by the results in both studies as summarized below:

A. Turf quality, root growth and viability in Penncross declined with increasing temperatures to and above 30 C. Temperatures above 30 C also caused an imbalance between photosynthesis and respiration and carbon deficit, and reduced carbohydrate availability

B. Turf quality and root activity were much lower at high root (20/35) or shoot/root (35/35 C) temperature than at a low shoot/root temperature (20/20 C) for all cultivars. Reducing root temperature to 20 C while maintaining shoots at 35 C improved turf quality and root growth to levels similar to those of the control treatment.

C. High shoot/root temperatures reduced canopy photosynthetic rate, caused imbalance between photosynthesis and respiration, and carbon deficit, whereas reducing root temperatures resulted in net carbon gain.

D. The decline in turf quality was more severe for Penncross than Crenshaw, L-93 and Penn A-4 under high root or shoot/root temperatures. Similarly, the daily carbon consumption to carbon production ratio was higher for Penncross than other cultivars under high root or shoot/root temperature conditions.

E. Extending mowing frequency from daily to every other day improved turf quality and root growth, especially under high root or shoot/root temperatures, which was accompanied by enhanced photosynthetic rate and reduced carbon consumption to production ratio.

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Knievel, D.P. 1973. Procedure for estimating ratio of live to dead root dry matter in root core samples. Crop Sci. 13:124-126.

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Personnel involved in the project

Postdoctoral research associate, Qingzhang XU. Percent effort -100%
Two part-time student labors (about 30 h each week)
Bingru Huang (PI). Percent effort - 20%
Jack D. Fry (Co-PI). Percent effort - 5%

Publications related to this project

Two manuscripts are being prepared to be submitted for publication in Crop Science by the end of this year. Another manuscript will be submitted early 1999.

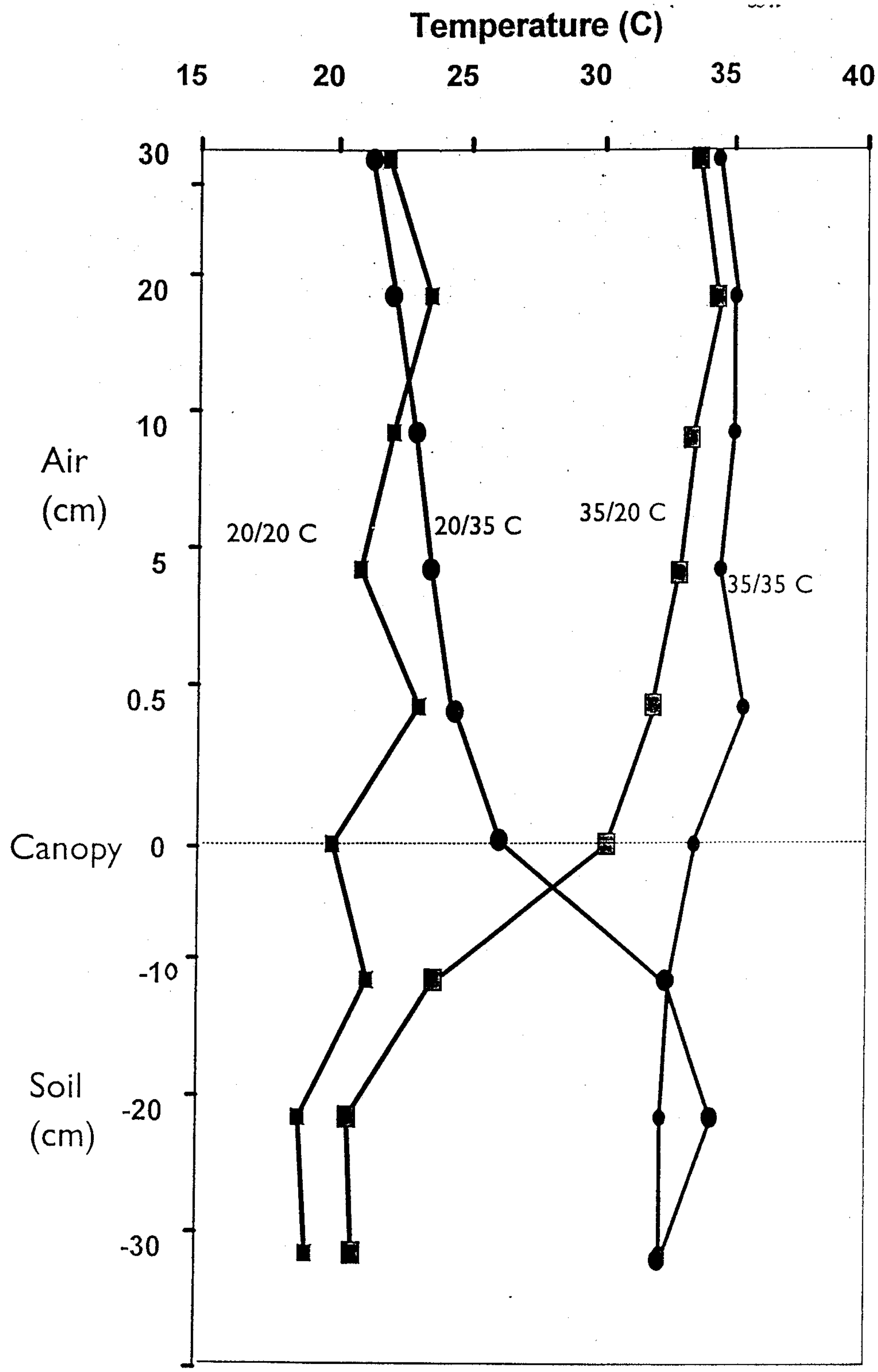


Fig. 1. Air temperature at different distances above the soil surface, as indicated by the dotted line, canopy temperature, and soil temperature at different depths below the soil surface under four shoot/root temperature regimes.

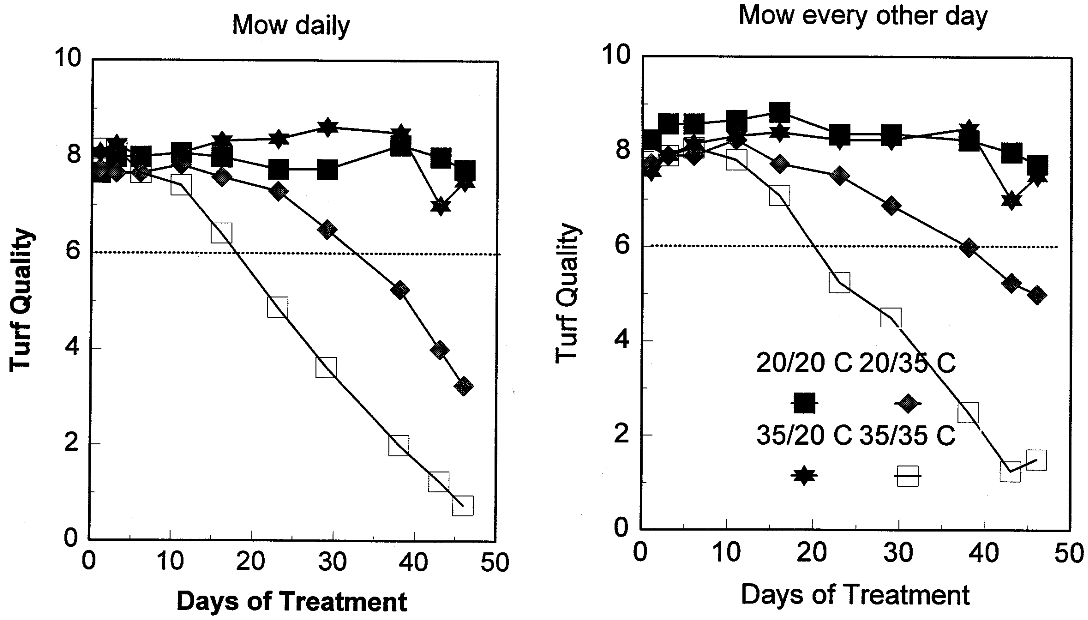


Fig. 2. Turf quality of Penncross as affected by differential shoot/root temperatures and mowing frequency. Dotted lines indicate the acceptable level of visual quality.

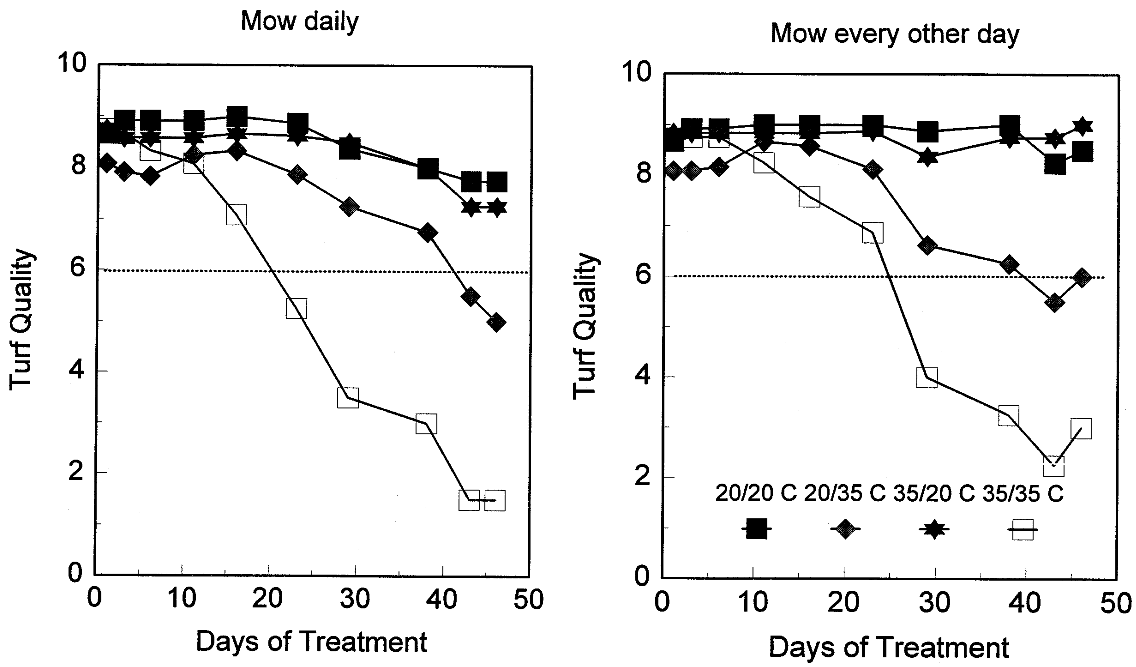


Fig. 3. Turf quality of Penn A-4 as affected by differential shoot/root temperatures and mowing frequency. Dotted lines indicate the acceptable level of visual quality.

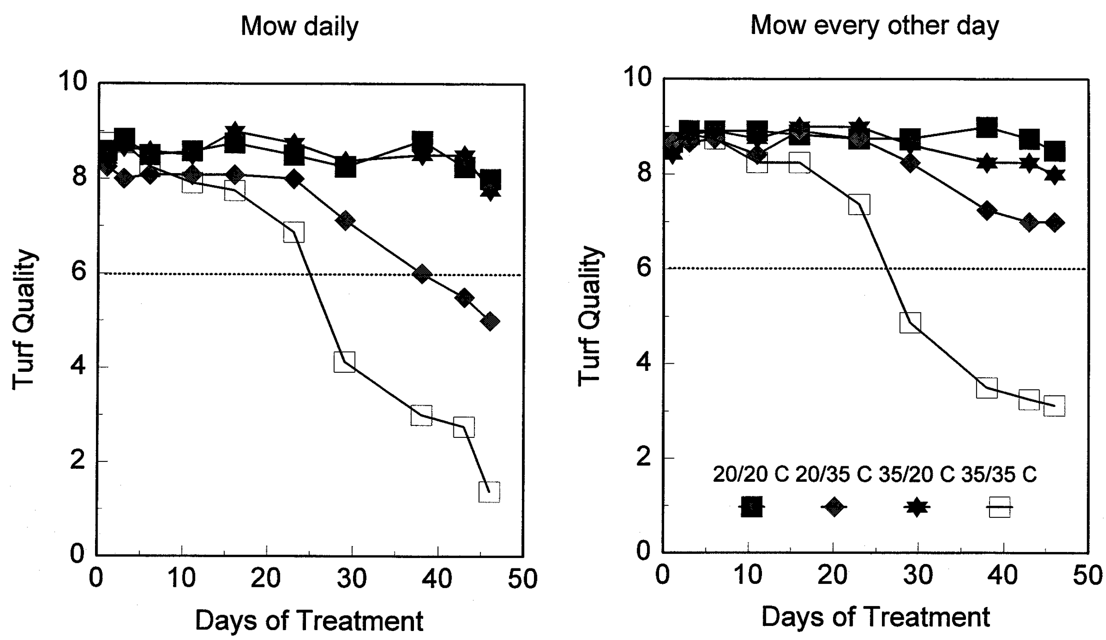


Fig. 4. Turf quality of Crenshaw as affected by differential shoot/root temperatures and mowing frequency. Dotted lines indicate the acceptable level of visual quality.

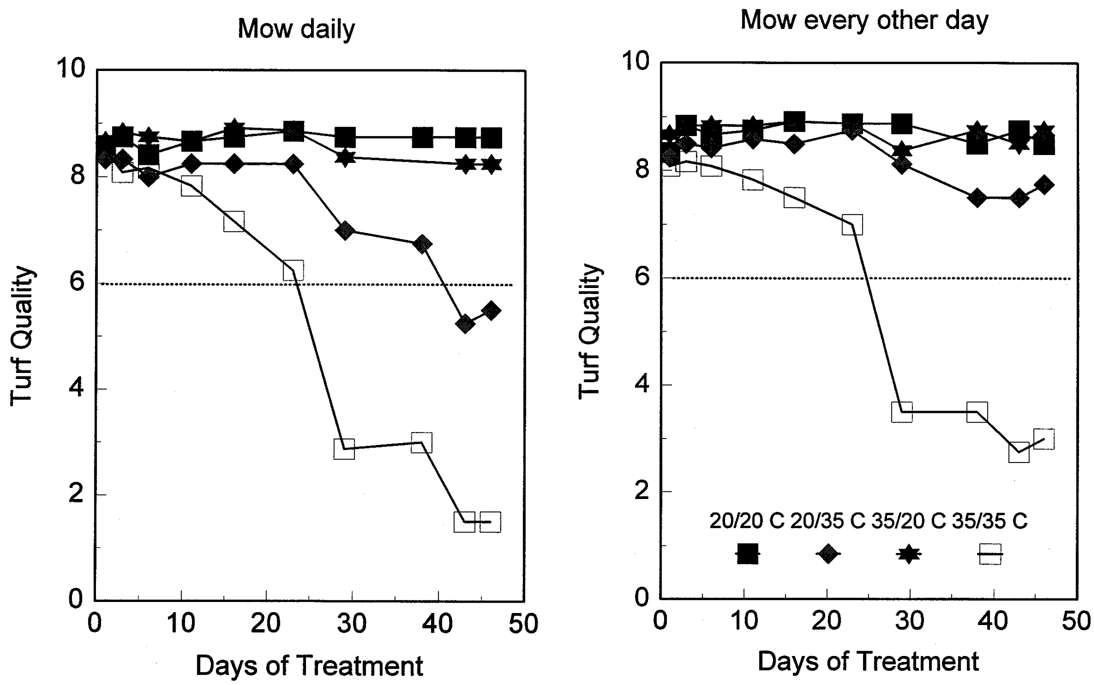


Fig. 5. Turf quality of L-93 as affected by differential shoot/root temperatures and mowing frequency. Dotted lines indicate the acceptable level of visual quality.

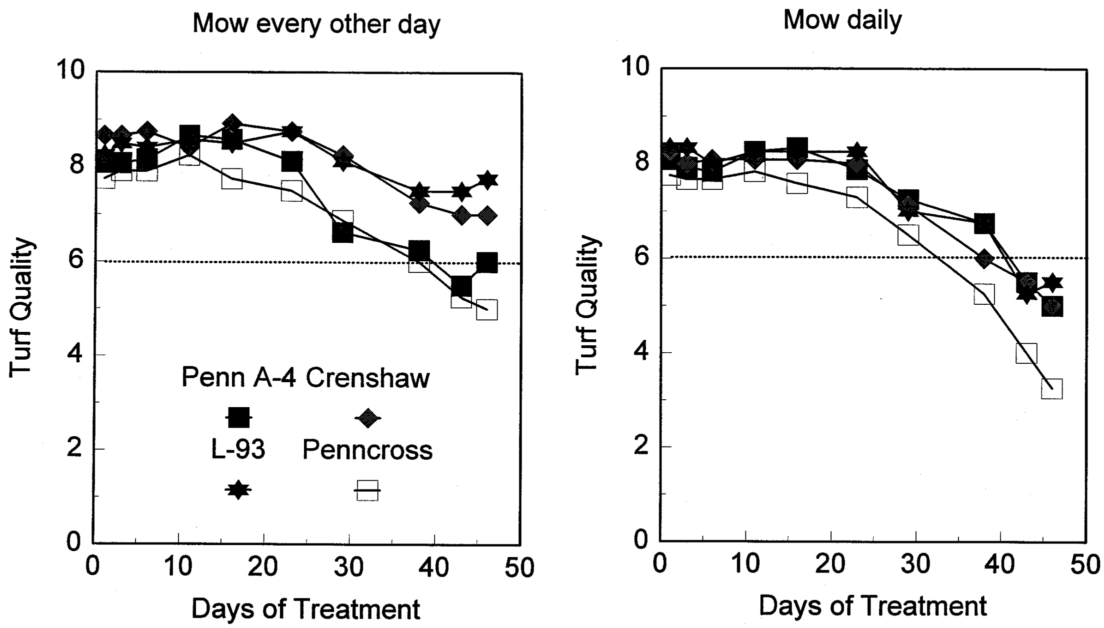


Fig. 6. Turf quality of four bentgrass cultivars grown at high root temperatures (20/35 C) when mowed daily or on alternate days. Dotted lines indicate the acceptable level of visual quality.

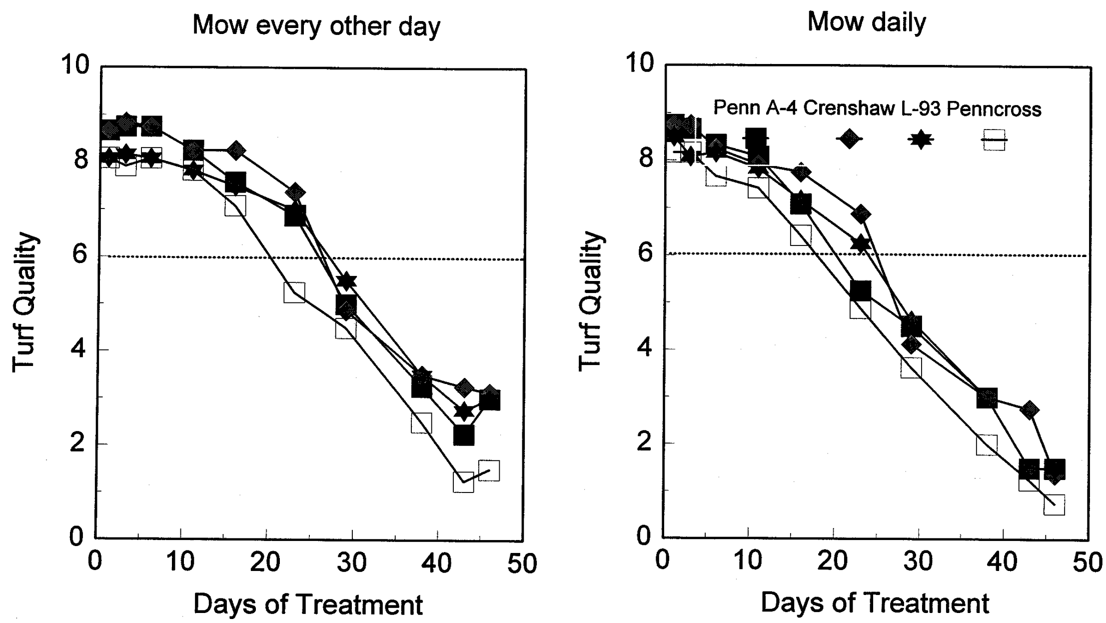


Fig. 7. Turf quality of four bentgrass cultivars grown at high shoot/root temperatures (35/35 C) when mowed daily or on alternate days. Dotted lines indicate the acceptable level of visual quality.

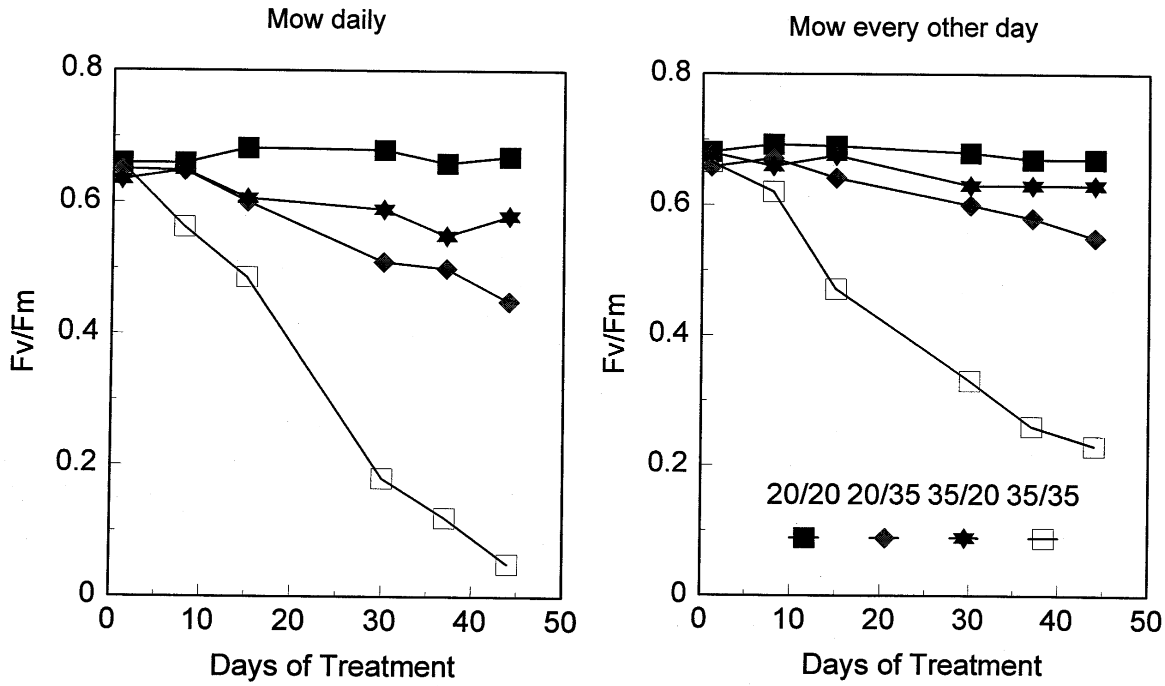


Fig. 8. Photochemical efficiency of Penncross as affected by differential shoot/root temperatures and mowing frequency

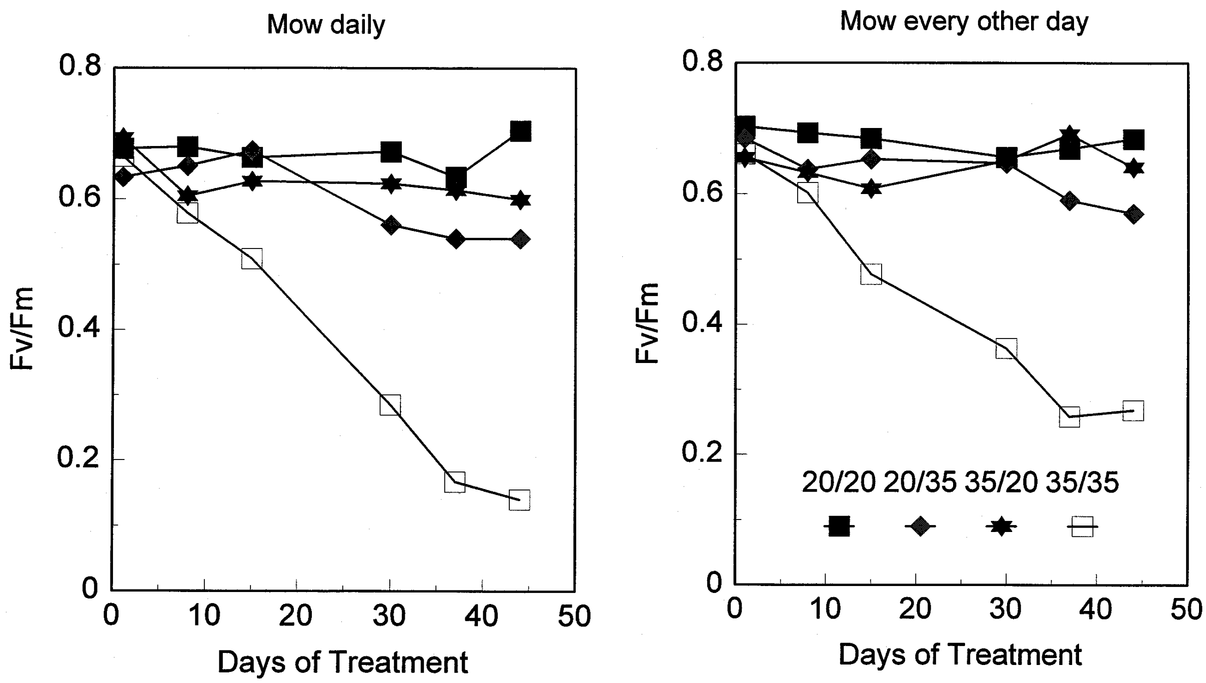


Fig. 9. Photochemical efficiency of Penn A-4 as affected by differential shoot/root temperatures and mowing frequency

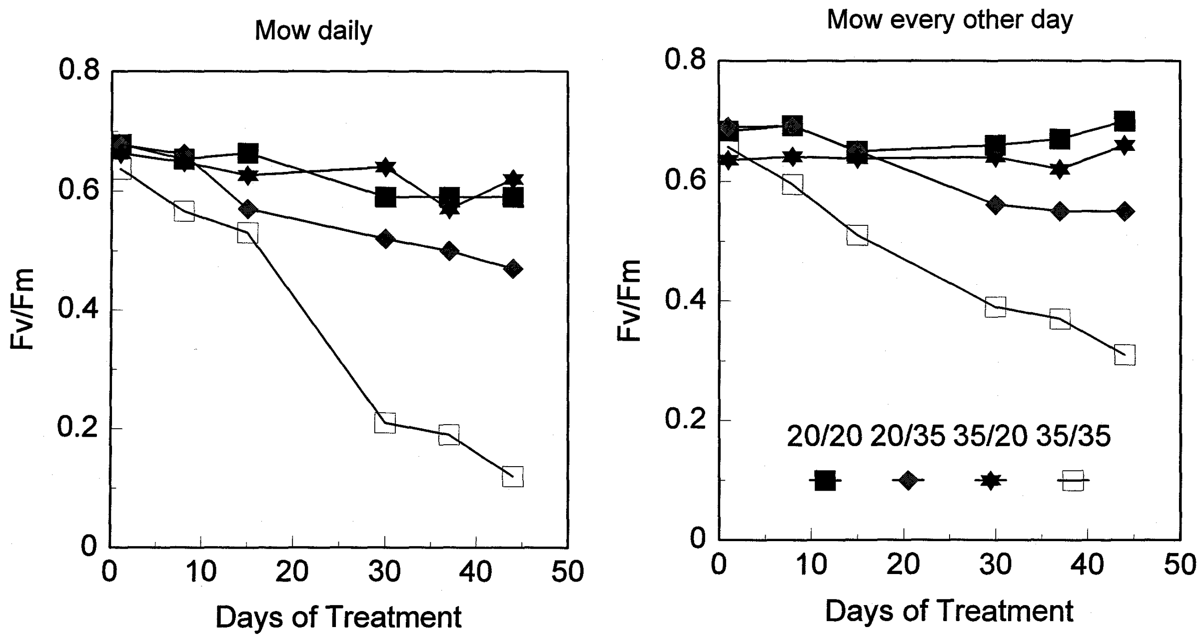


Fig. 10. Photochemical efficiency of Crenshaw as affected by differential shoot/root temperatures and mowing frequency

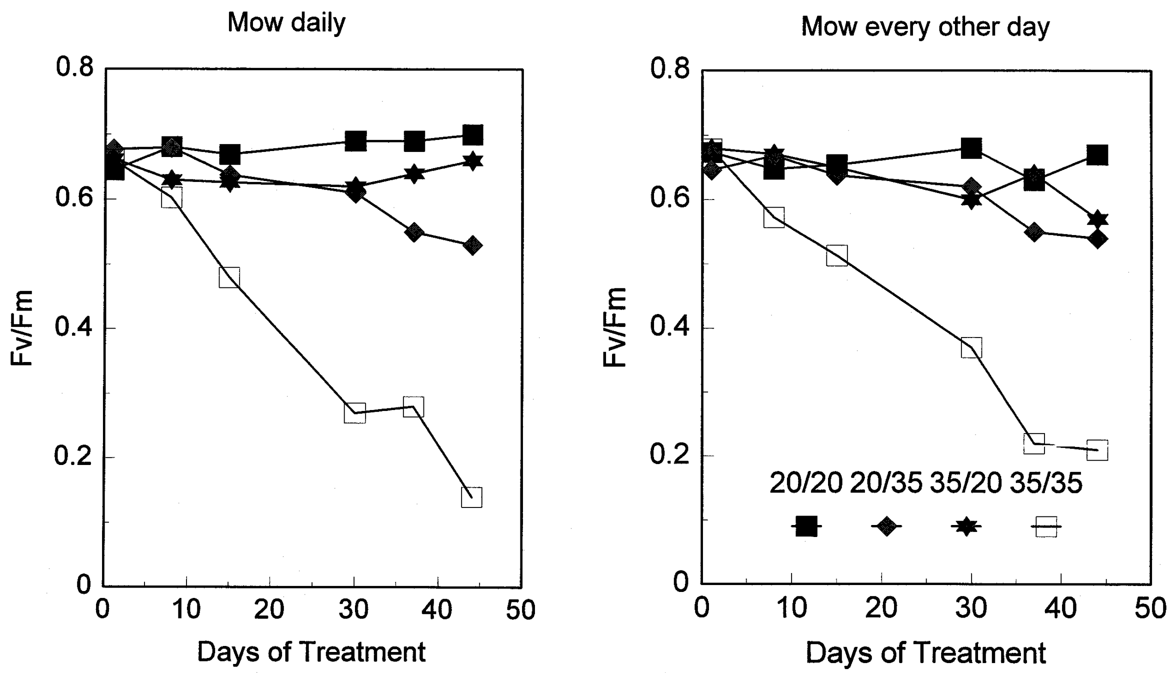


Fig. 11. Photochemical efficiency of L-93 as affected by differential shoot/root temperatures and mowing frequency

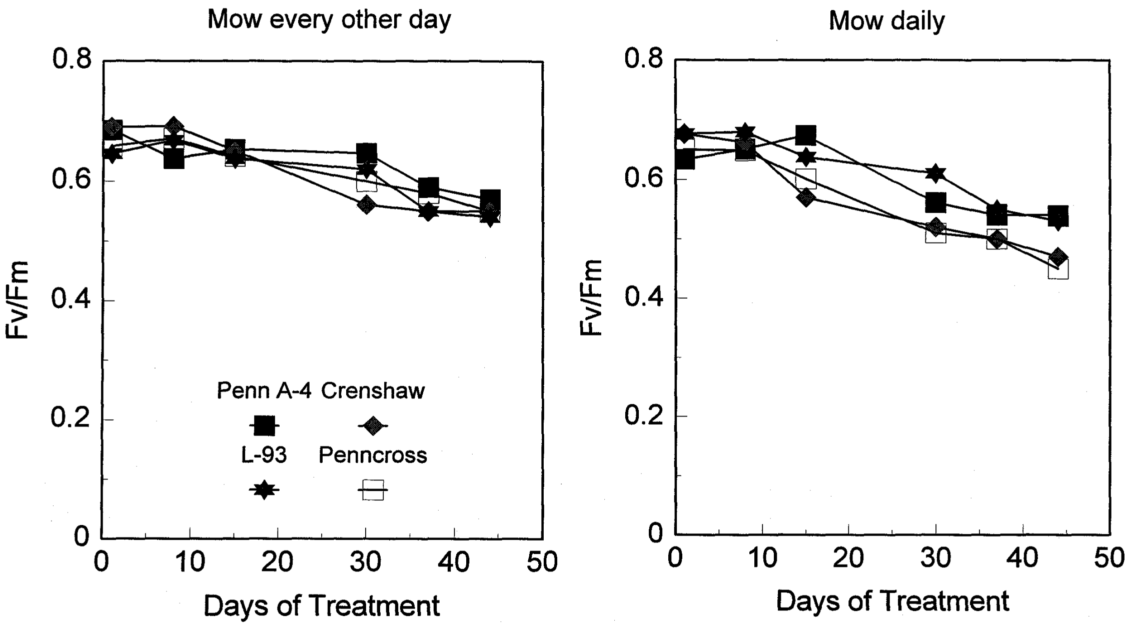


Fig. 12. Photochemical efficiency of four bentgrass cultivars grown at high root temperature (20/35 C) when mowed daily or on alternate days

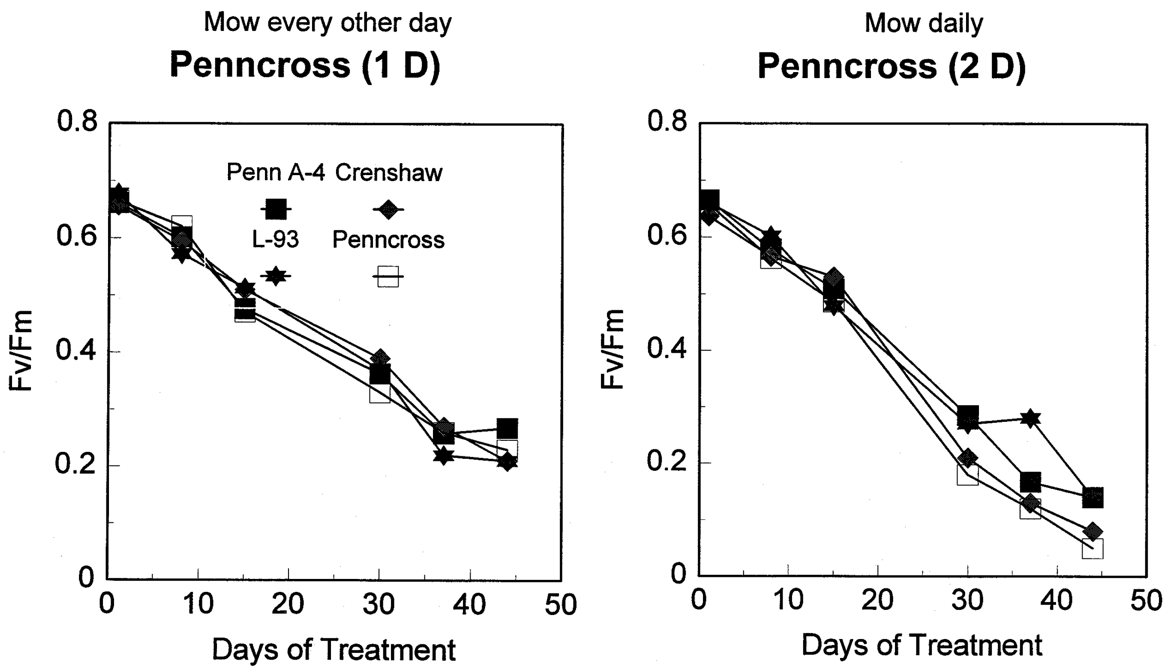
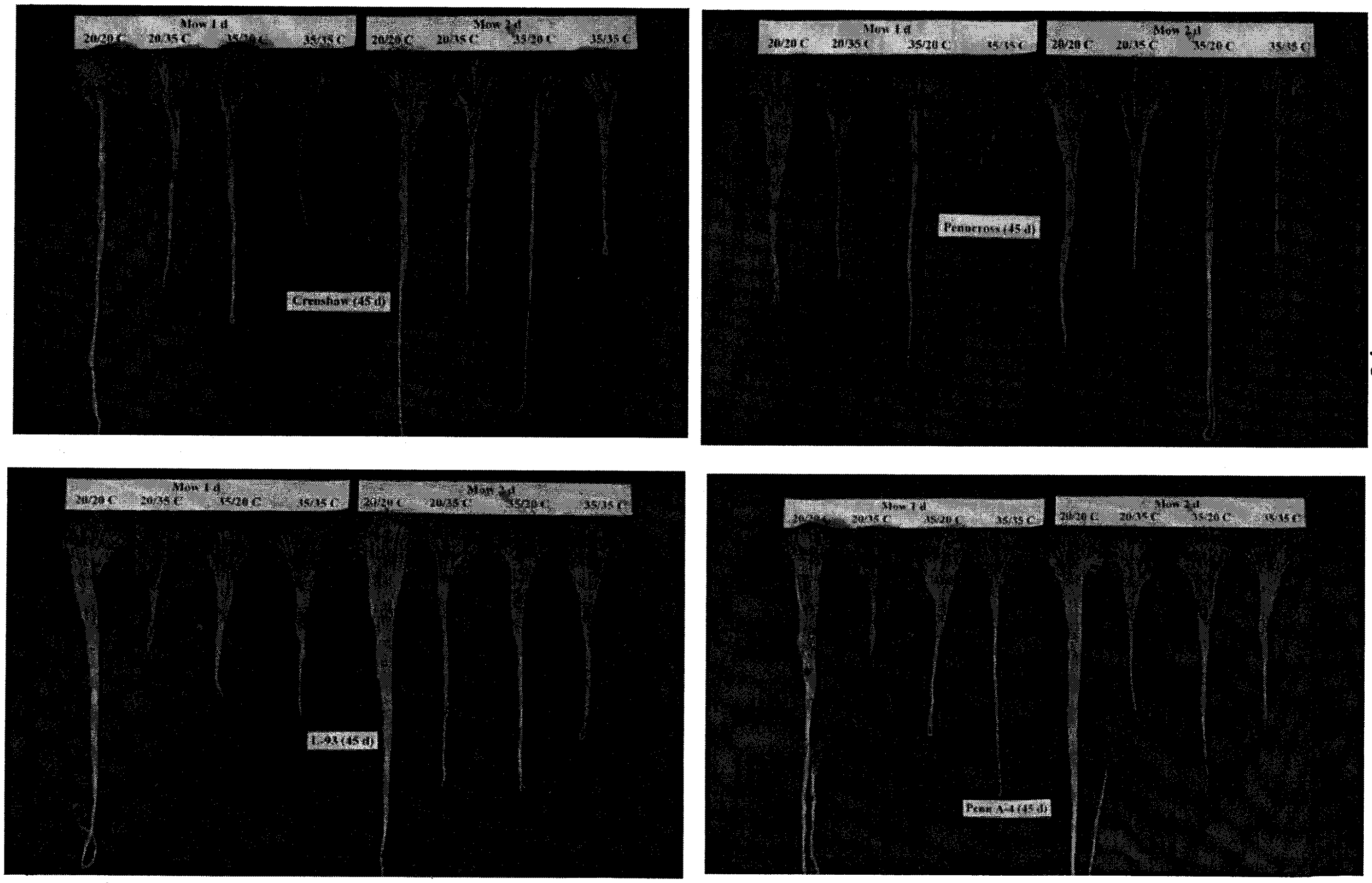


Fig. 13. Photochemical efficiency of four bentgrass cultivars grown at high shoot/root temperature (35/35 C) when mowed daily or on alternate days

Fig. 14. Root growth as affected by differential shoot/root temperatures and mowing frequency



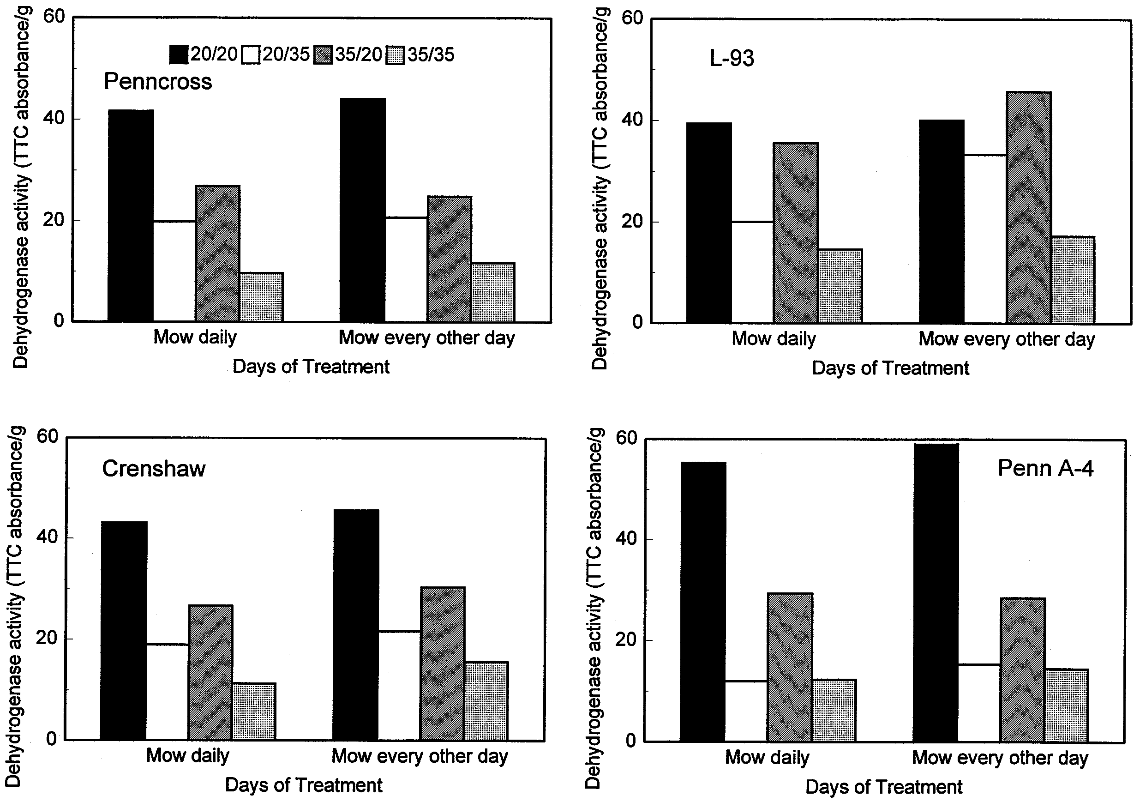


Fig. 15. Root viability affected by differential shoot/root temperatures and mowing frequency.

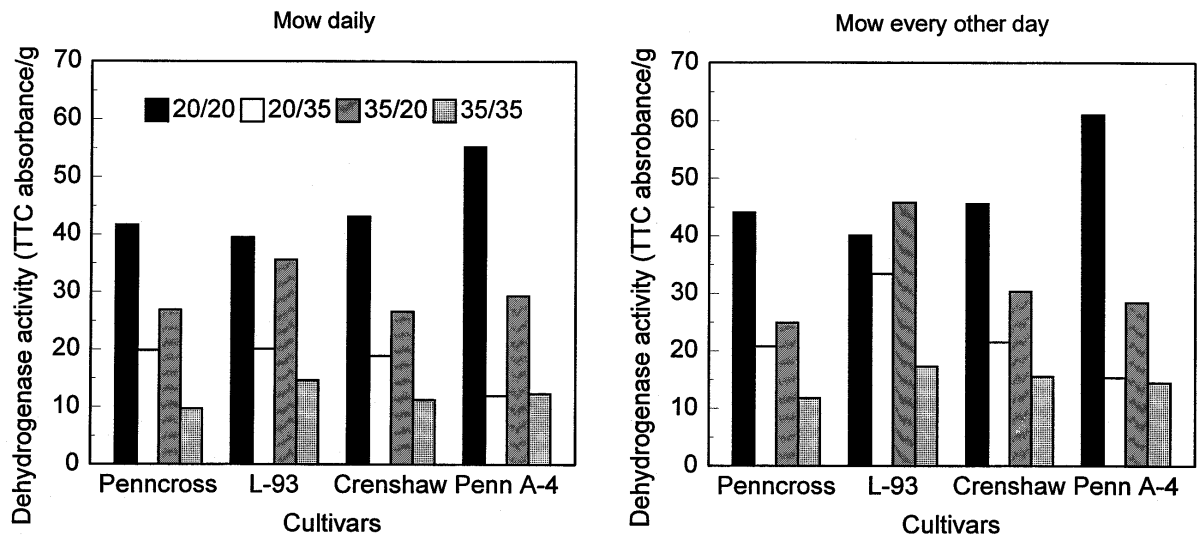


Fig. 16. Root viability affected by differential shoot/root temperatures and mowing frequency

Mow daily

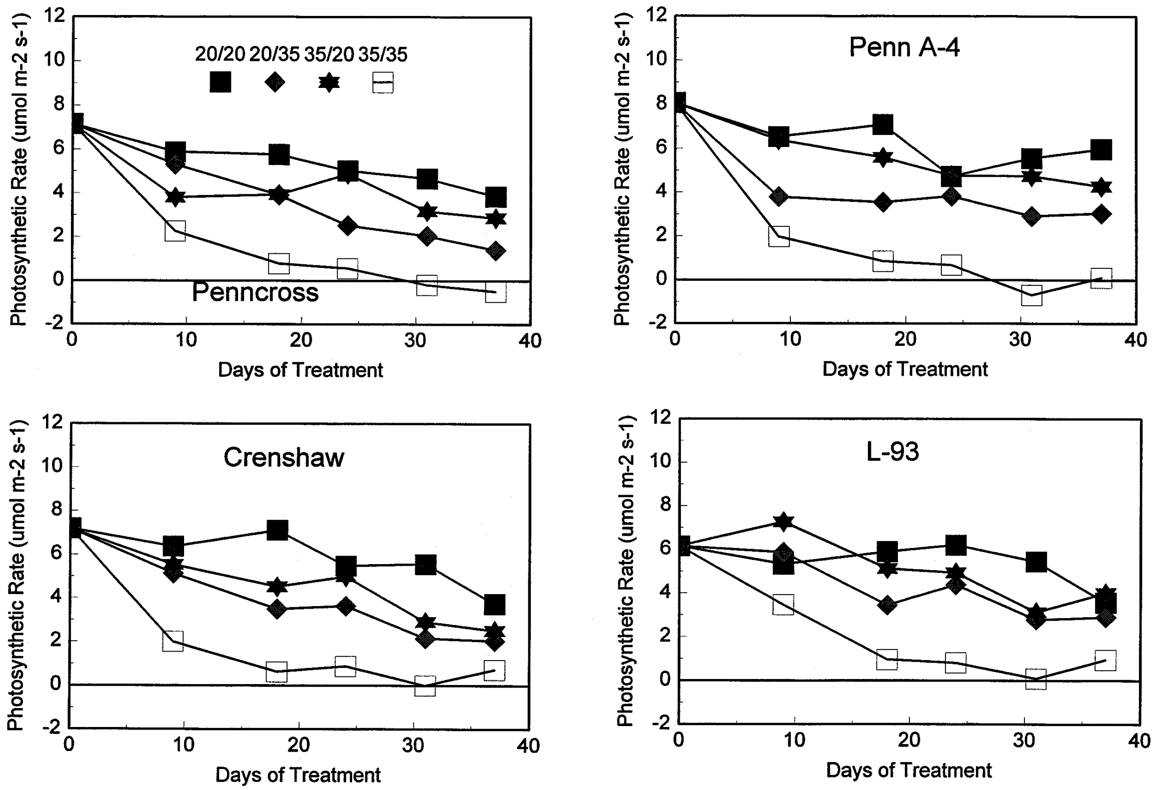


Fig. 17. Canopy photosynthetic rate of four bentgrass cultivars as affected by differential shoot/root temperatures when mowed daily

Mow every other day

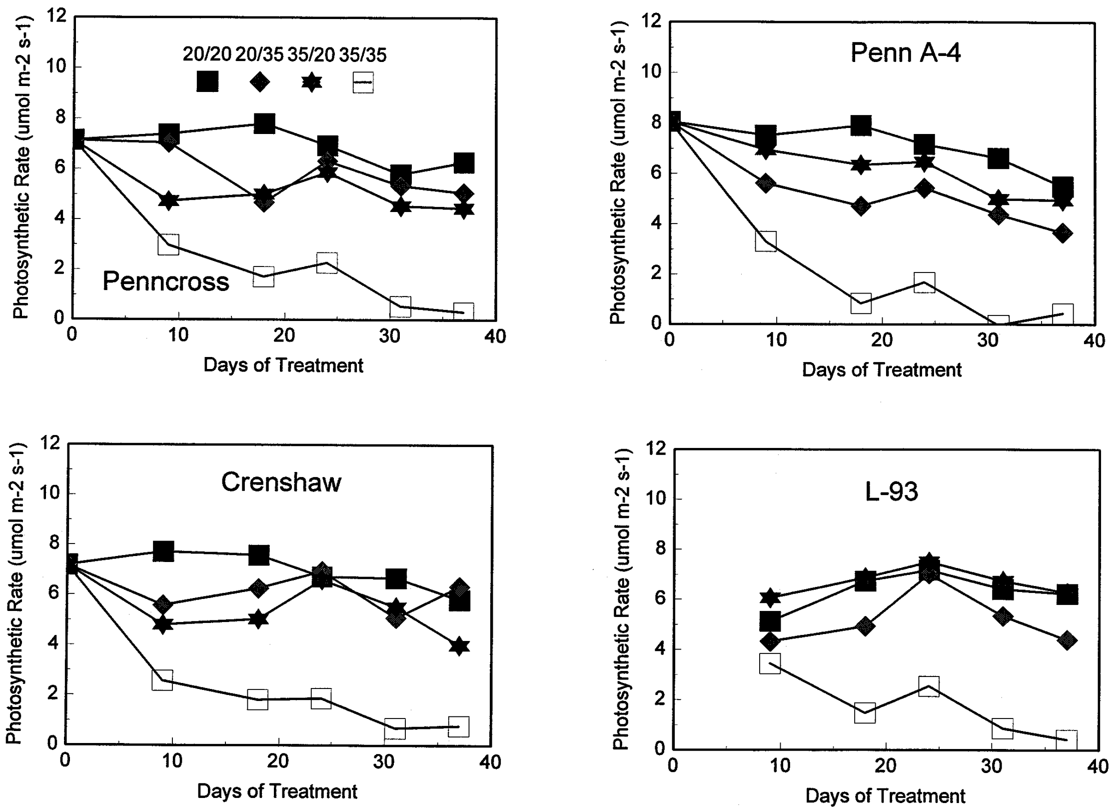


Fig. 18. Canopy photosynthetic rate of four bentgrass cultivars as affected by differential shoot/root temperatures when mowed on alternate days.

Mow daily

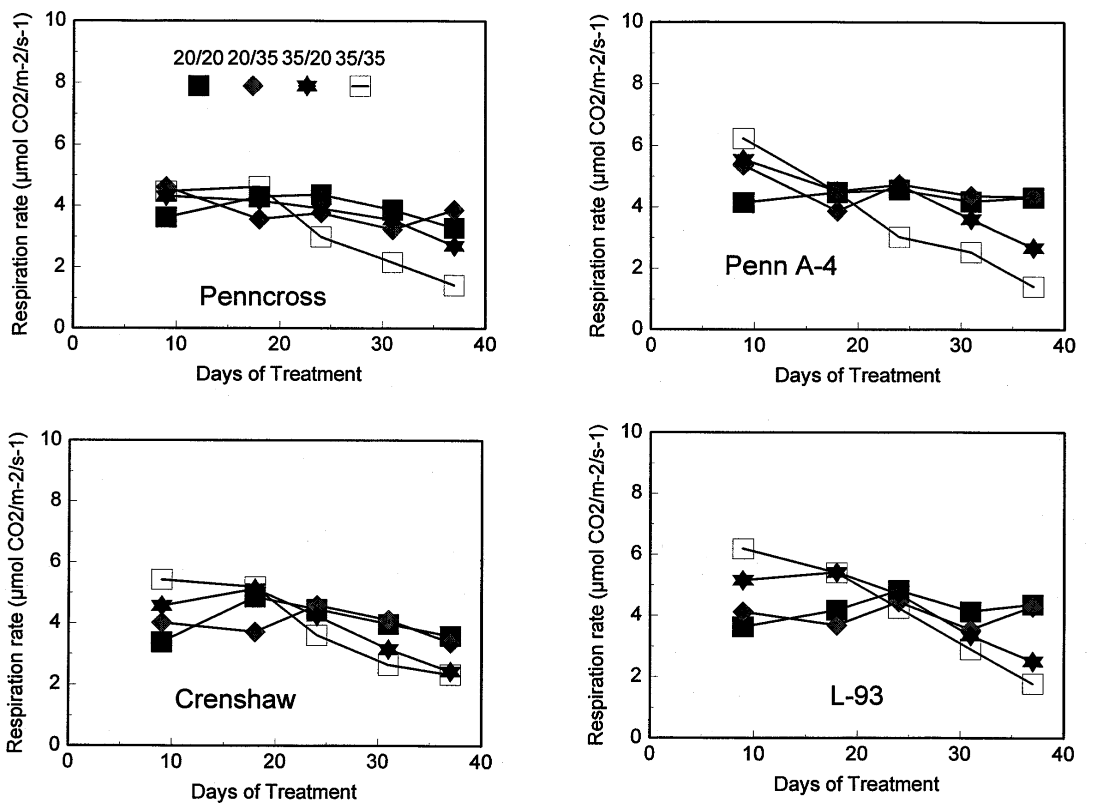


Fig. 19. Whole plant respiration rate of four bentgrass cultivars as affected by differential shoot/root temperatures when mowed daily.

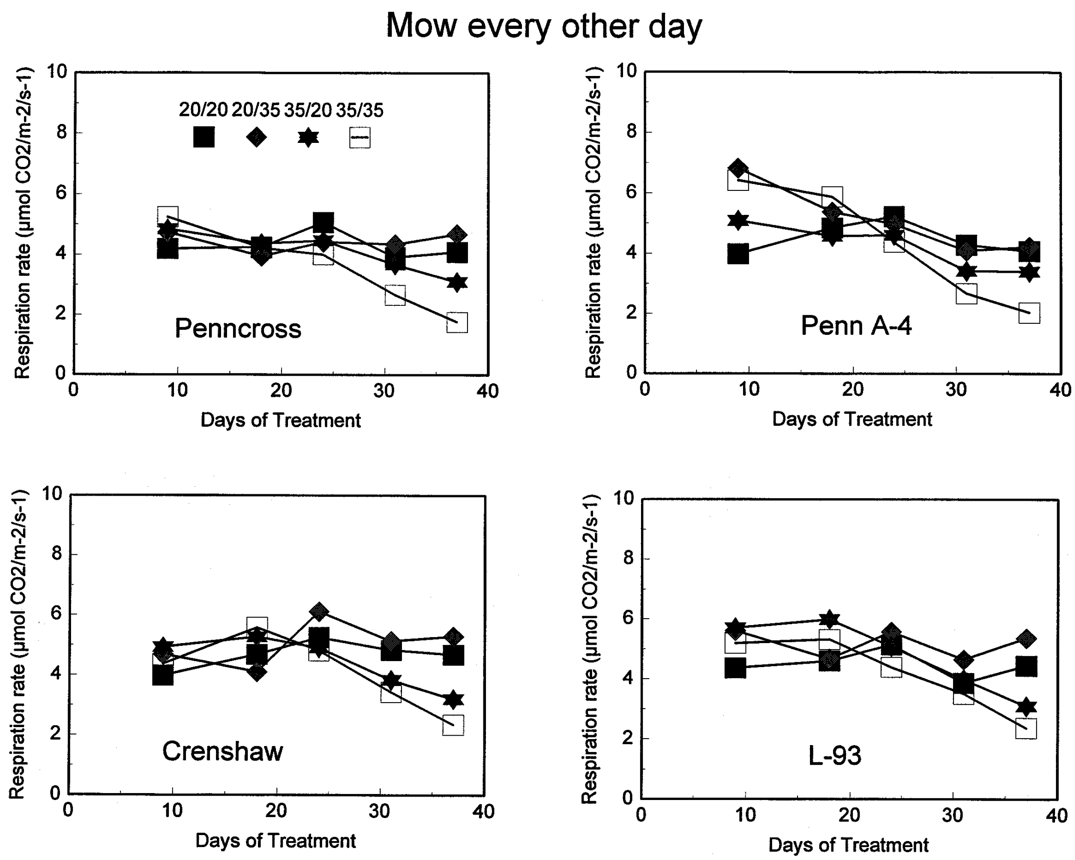


Fig. 20. Whole plant respiration rate of four bentgrass cultivars as affected by differential shoot/root temperatures when mowed on alternate days.

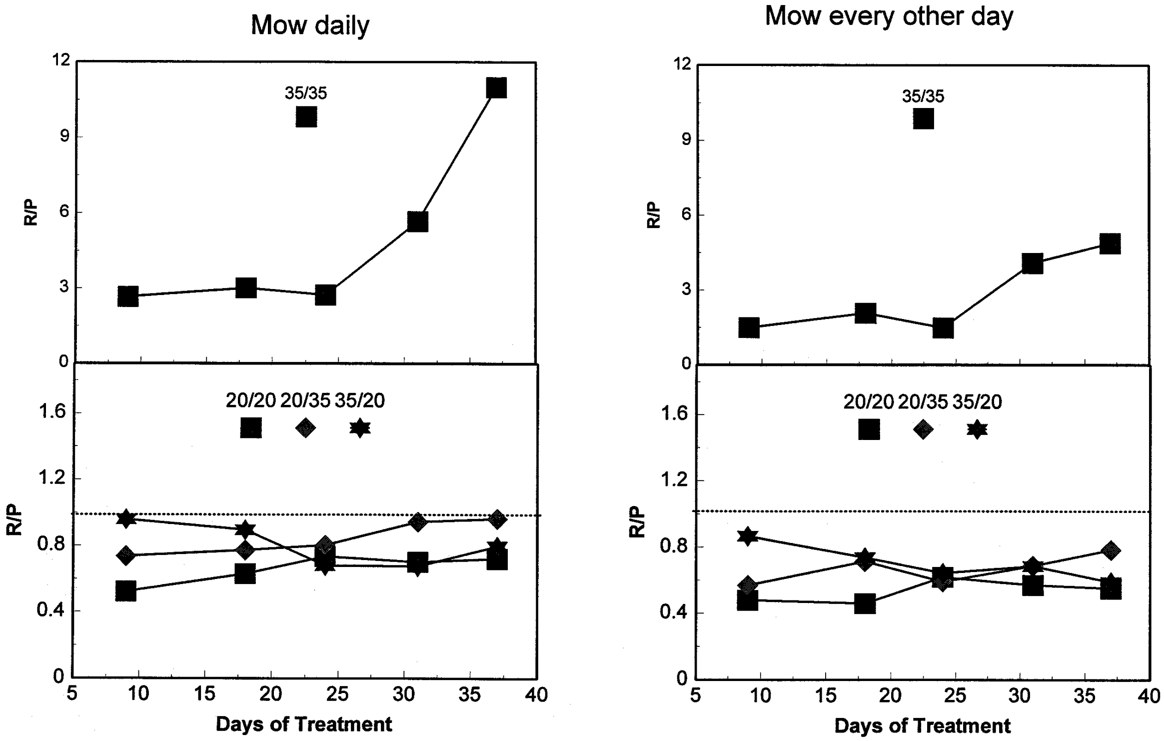


Fig. 21. Daily carbon consumption (R) as a proportion of carbon production (P) for Penncross when grasses mowed daily or on alternate days. Dotted lines indicate where the R/P ratio is 1.

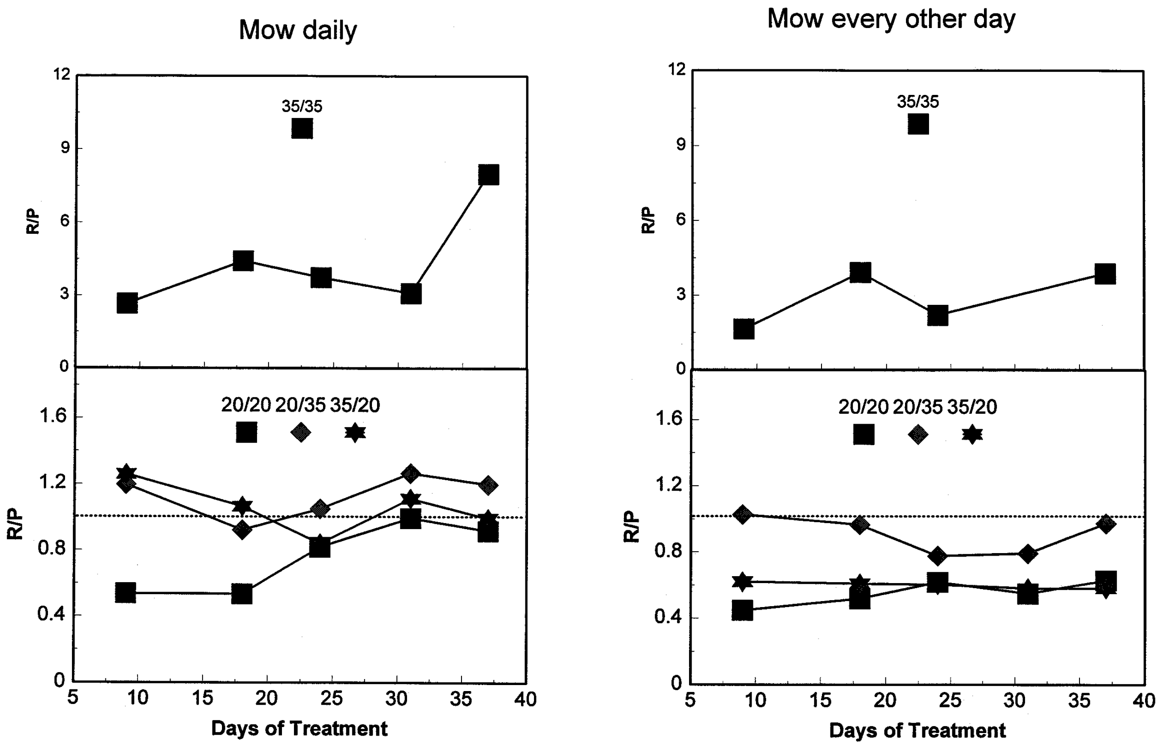


Fig. 22. Daily carbon consumption (R) as a proportion of carbon production (P) for Penn A-4 when grasses mowed daily or on alternate days. Dotted lines indicate where the R/P ratio is 1.

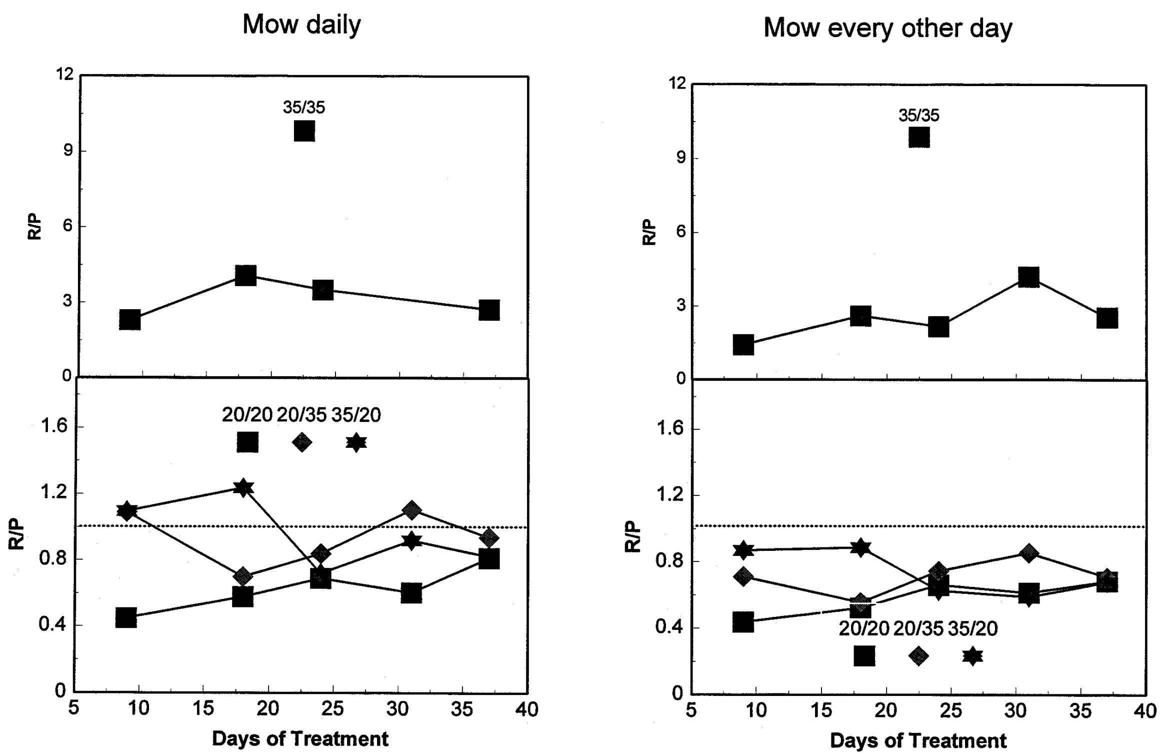


Fig. 23. Daily carbon consumption (R) as a proportion of carbon production (P) for Crenshaw when grasses mowed daily or on alternate days. Dotted lines indicate where the R/P ratio is 1.

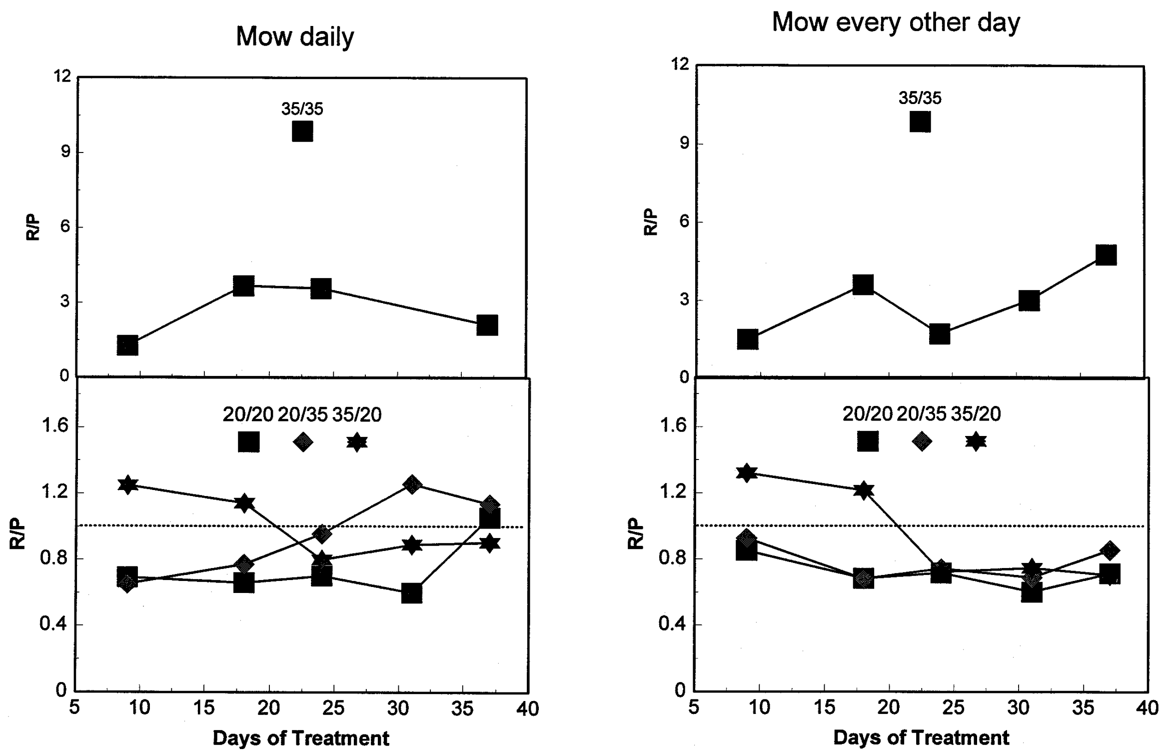


Fig. 24. Daily carbon consumption (R) as a proportion of carbon production (P) for L-93 when grasses mowed daily or on alternate days. Dotted lines indicate where the R/P ratio is 1.

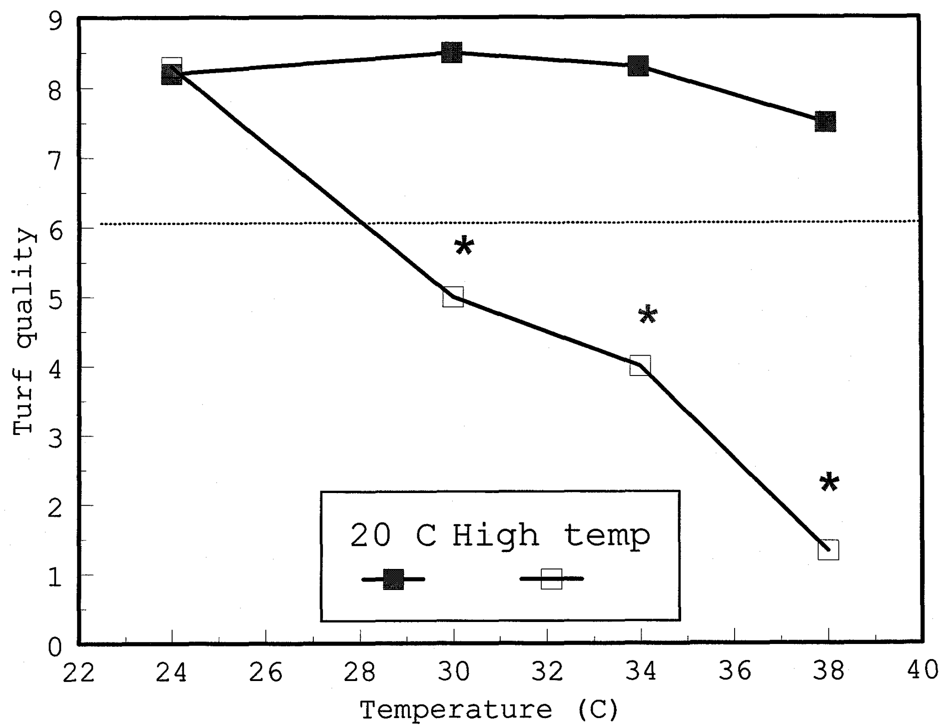


Fig. 25. Turf visual quality in response to increasing temperature for Penncross. Dotted line indicates the acceptable level of visual quality. * indicates the treatments were significantly different at p=0.05.

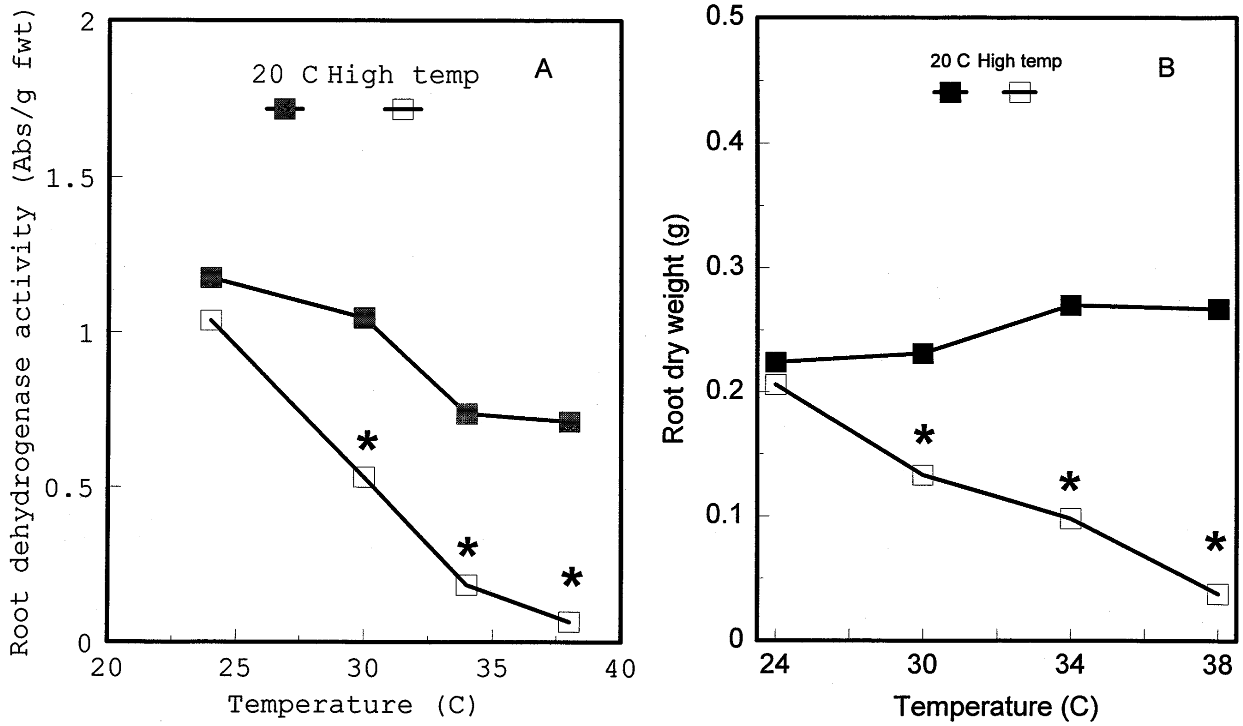


Fig. 26. Root growth and viability in response to increasing temperature for Penncross.
* indicates the treatments were significantly different at p=0.05.

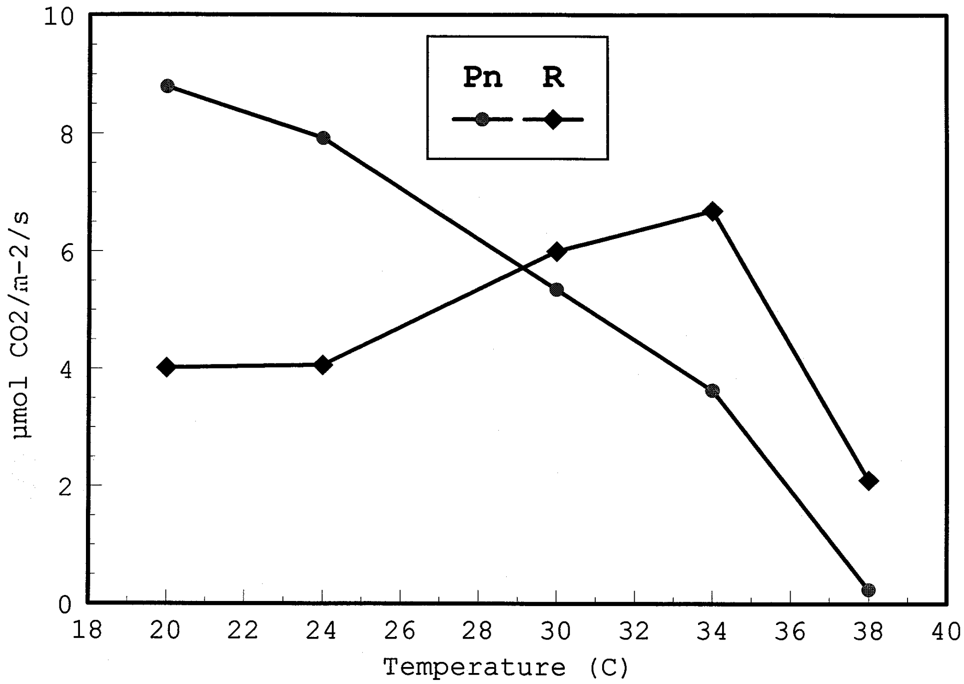


Fig. 27. Canopy photosynthetic rate (Pn) and respiration rate (R) in response to increasing temperature for Penncross.

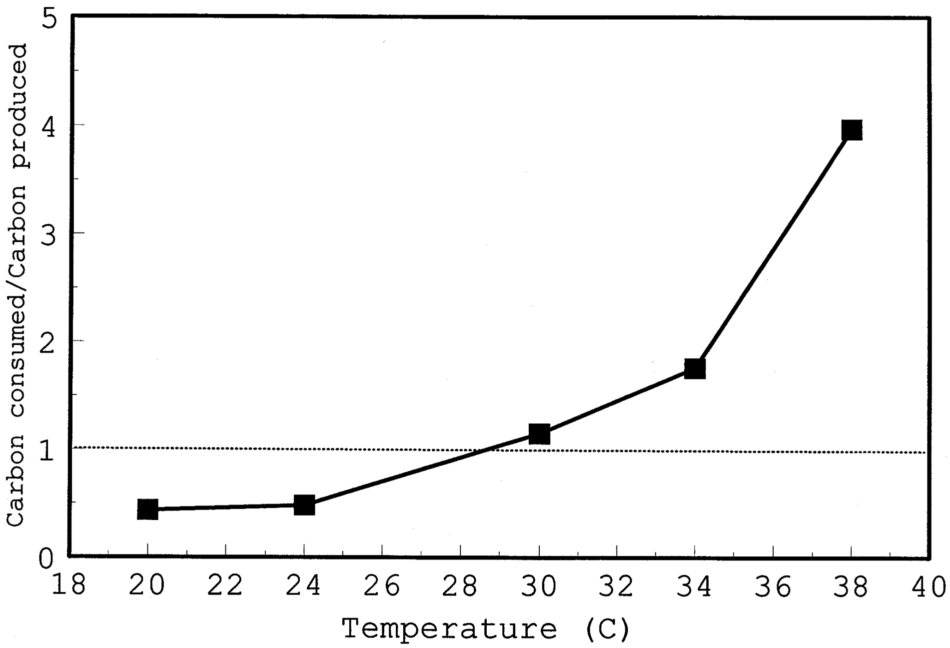


Fig. 28. Daily carbon consumption as a proportion of daily carbon production in response to increasing temperature for Penncross. Dotted line indicates where the carbon consumption to production ratio is 1.

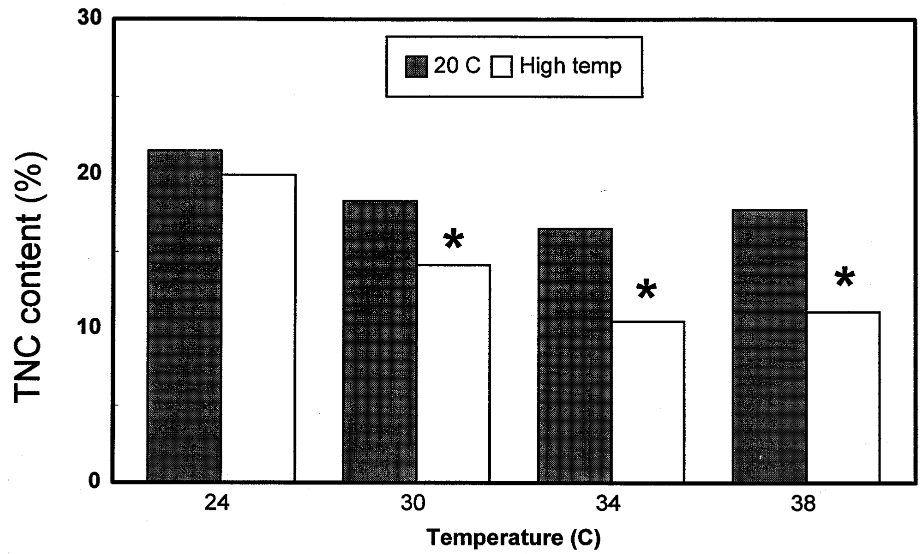


Fig. 29. Carbohydrate accumulation of shoots in response to increasing temperature for Penncross. * indicates treaments were significantly different at p=0.05.