

TURFGRASS PHOTOSYNTHESIS: A REVIEW

Photosynthesis is the only significant process through which non-nutritious inorganic compounds are converted into essential foodstuffs for plants. The plants then become available for human and animal consumption and in the case of turfgrasses, recreation. An understanding of photosynthesis and conditions which control it are important in all plant science disciplines and a review of the literature is essential in gaining this understanding. The intent of this paper is to review the literature for photosynthetic research pertaining to turfgrass species and cultural practices. This review is primarily confined to scientific journal articles and will contains literature which refers to grass species used both in turfgrass and forage management.

ENVIRONMENTAL EFFECTS

Light. Cooper and Wilson (13) reported photosynthetic saturation at 20,000-30,000 lux for annual (*Lolium multiflorum* Lam.) and perennial (*L. perenne* L.) ryegrass. Photosynthetic saturation for creeping bentgrass (*Agrostis palustris* Huds. or *A. stolonifera* var. *palustris* (Farwell)) has been reported to be about $500 \mu\text{mol m}^{-2} \text{ s}^{-1}$ (53).

Alexander and McCloud (3) reported maximum photosynthesis for isolated leaves of bermudagrass (*Cynodon dactylon* (L.) Pers.) at 2500 to 3000 foot-candles, with a light compensation point of 300 foot-candles. Growth of red fescue (*Festuca rubra* L.) and Kentucky bluegrass (*Poa pratensis* L.) at low light intensities resulted in a low carbon dioxide exchange rate (CER), when measured at saturating or growth-condition light levels (71). Winstead and Ward (74) studied the CER of warm season turfgrasses in shade and found bermudagrass to display a decrease in CER under shade while St. Augustinegrass (*Stenotaphrum secundatum* (Walt.) Kuntze) showed a slight increase. Morgan and Brown (46) investigated light response in Coastal bermudagrass and reported the response of CER to photosynthetic photo flux density (PPFD) followed a rectangular hyperbola with the curves becoming more linear and maximum CER increasing as leaf area index (LAI) increased. It has been shown that saturation (i. e. maximum photosynthesis) requires greater levels of ambient light under simulated swards than that required for saturation of individual bermudagrass leaves and that swards with a height of eight and 14 inches (before mowing) required a lower ambient light level for saturation than swards at 20 and 26 inches (3). Dienum (16) demonstrated that shading and defoliation of the axillary tillers of vegetative annual ryegrass plants stimulated leaf photosynthesis of the main shoot which coincided with a lower stomatal and internal

diffusive resistance and lower soluble carbohydrate content, suggesting that the stressed tillers function as sinks for the assimilates. Woledge (77) showed that as the leaf area of swards of perennial ryegrass increased, successive leaves which expanded on the main stem of the sample plant within the sward had progressively lower photosynthetic capacities, postulated to be due to the newer leaves expanding under lower illumination levels. Further work by Woledge (76) showed that this decline in photosynthesis could be prevented by protecting tillers from shading during growth. Woledge (75) measured higher photosynthesis in the leaves of reproductive tillers and concluded that this increase was because stem extension carries these leaves to the top of the canopy where they are well illuminated during expansion. Meadow fescue (*Festuca pratensis* Huds.) when grown at two light intensities had higher CER in plants preconditioned at the higher light intensity (42).

Temperature. Miller (44) measured the rate of apparent photosynthesis in Seaside creeping bentgrass and Common bermudagrass at six temperatures. The relative rate of photosynthesis for creeping bentgrass increased from 65% at 15 °C to a maximum of 100% at 25°, then decreased to 62% at 40 °C. The relative rate for bermudagrass increased from 55% at 15 °C to a maximum of 100% at 35° and dropped to only 98% of maximum at 40 °C. Schmidt and Blaser (61) reported a 172% increase in net photosynthesis in Tifgreen bermudagrass (*Cynodon dactylon* X *C. transvaalensis*) when measured at 24

°C vs. 12 °C and a 96% increase when measured at 24 °C vs. 36 °C. Watschke et al. (69) found that growth for three weeks at 35 °C reduced the net photosynthesis of eight cool season turfgrass cultivars, when compared to growth at 23 °C. Rogers et al. (57) reported no significant differences in CER, based on unit land area, between three *Zoysia* spp. and three bermudagrass cultivars when measured during cold hardening. Woledge and Parsons (81) showed that as ambient temperature increased from 10 to 25 °C canopy photosynthesis in a sward of perennial ryegrass increased. Woledge and Dennis (78) found that growth temperature had little effect on the rate of leaf photosynthesis in perennial ryegrass, but measurement temperature strongly influenced assimilation, with rates measured at 15 °C being twice those at 5 °C. A similar response has been shown in tall fescue (*Festuca arundinacea* Schreb.) (79). Pammentor (53) reported the optimal temperature range for CER in creeping bentgrass to be between 15 and 25 °C. Schmidt and Blaser (62) measured the net photosynthesis of Cohensey bentgrass at three temperatures and found that 80% more CO₂ was fixed at 24 vs. 12 or 36 °C. Duff and Beard (20) found that preconditioning creeping bentgrass at supraoptimal temperatures increased photosynthesis. Plants preconditioned at 30-40 °C had significantly higher photosynthetic rates than plants at 25-35, 20-30, or 15-25 °C. The lowest photosynthetic rate was in plants preconditioned at 10-20 °C. All plants were measured at the

highest range of their growth temperature. When plants grown at 10-20 or 30-40 °C were measured at temperatures of 20, 30 and 40 °C, the plants preconditioned at the higher temperature exhibited a higher photosynthetic rate at all three test temperatures. Davidson and Robson (15) found no difference in canopy photosynthetic rate ($\text{g CO}_2 \text{ m}^{-2} \text{ h}^{-1}$) for perennial ryegrass plants preconditioned and measured at either high (20 °C day/15 °C night) or low (10 °C day/8 °C night) temperature. Labhart et al. (42) found preconditioning temperature to have no effect on CER in meadow fescue. Murata and Iyama (48) found maximum photosynthesis for annual and perennial ryegrass to occur around 10 °C, with a steep decline after 25 °C, while bermudagrass and bahairgrass (*Paspalum notatum* Flugge.) had photosynthetic maximums near 35 °C. Ollerenshaw et al. (50) found a cold adapted selection of red fescue to have a higher photosynthetic rate than a less cold adapted selection, when assimilation was measured at 2 °C. The CER of two bermudagrass cultivars (Ormond and Pee Dee) and two St. Augustinegras cultivars (Texas Common and Floratam) was monitored continuously for 14 days at chilling temperatures (day/night, 7/5 °C, respectively) by Karnok and Beard (35). Ormond, Pee Dee, Texas Common, and Floratam showed reductions of 54, 68, 79, and 84%, respectively, in daytime CER during the initial chilling period.

Carbon Dioxide. Krenzer and Moss (39) measured the CO_2 compensation points for 325 species of Graminaea. In

general species in the *Festucoideae* subfamily had high compensation points and those in the subfamily *Panicoideae* low compensation values. The CO₂ compensation points for nineteen species of Graminaea was measured by Downton and Tregunna (19) with all C₄ species having low (<5 ppm) and C₃ species having high (37-50 ppm) compensation points. However, bermudagrass (compensation point 5 ppm) was the only turf species evaluated. Imai et al. (31) found zoysiagrass (*Zoysia japonica* Steud.) to have a CO₂ compensation point of 1 ppm. Brown and Brown (6) reported a CO₂ compensation point of 54 ppm for tall fescue. Watschke et al. (69) found that preconditioning eight cool season turfgrass cultivars at 35 vs. 23 °C increased the CO₂ compensation point, while preconditioning temperature did not effect the compensation point of bermudagrass. Beard (5) reported that the microclimate under shade trees is higher in CO₂ than an unshaded area, which may affect photosynthesis.

Diurnal/Daylength. The effect of daylength on photosynthesis in annual bluegrass (*Poa annua* L.) and rough bluegrass (*Poa trivialis* L.) was investigated by Burian and Winter (9). Although short day conditions (8 h/16 h) decreased net production, the photosynthetic rate of short day grown plants was nearly twice as much as plants grown in long day (16 h/ 8 h) conditions. Application of red light early or in the middle of the dark period further increased the photosynthetic rate of short day plants and decreased

the rate in long day plants. Far-red light applied in the middle of the dark period produced the opposite effect. The authors concluded that the effect of red and far-red irradiation on chlorophyll synthesis did not sufficiently explain the apparent phytochrome dependent control of photosynthesis. Hay and Heide (27) reported that Kentucky bluegrass plants raised under short days gave significant increases in dry weight upon exposure to continuous light, compared with 8-h short days, at essentially identical daily inputs of radiant energy. This increase in relative growth rate was postulated to be due primarily to increased net assimilation rate followed, several days later, by increases in leaf area ratio when newly-emerged leaves began to constitute a significant portion of the leaf area. Murata and Iyama (47) found annual ryegrass to exhibit diurnal fluctuations in apparent photosynthesis. The fluctuations, however, coincided very closely to ambient CO₂ concentrations. Hansen (26) found root respiration in perennial ryegrass to exhibit diurnal fluctuations, with two characteristic peaks occurring 4-6 and 14-16 h after onset of the photoperiod, and respiration was dependent on net assimilation. Hull (30) measured diurnal variation in assimilate partitioning in Kentucky bluegrass and found that assimilate translocation from leaves to stems was more rapid in the morning than the afternoon, and translocation to roots was greater after noon. Rhizomes received little

photosynthate within the measurement period and exhibited no diurnal pattern.

Oxygen Inhibition. Brown and Brown (6) reported that an O₂ concentration of 21% reduced the net photosynthesis of tall fescue 40% when compared to an O₂ free environment. Downes and Hesketh (18) tested nearly 50 grass species for enhancement of photosynthesis in a low (< 1%) O₂ environment. All turfgrass species evaluated were C₃ types and included Kentucky bluegrass, annual ryegrass, and two *Agrostis* spp., with all showing significantly higher photosynthetic rates at the low O₂ condition. Watschke et al. found that the photosynthesis of cool season species approached that of bermudagrass when photorespiration was inhibited by low O₂ concentration (69), and that in 10 strains of Kentucky bluegrass low O₂ concentrations resulted in nearly a two-fold increase in net assimilation (70). Glacoleva and Zalensky (22) showed that in bermudagrass photosynthesis was higher at 21% vs. 1% O₂.

Post Illumination CO₂ Burst (PIB). The evolution of CO₂ upon the transition of leaves from light to darkness was studied in 44 grass species by Brown and Gracen (7). Turfgrass species tested which exhibited the PIB were bermudagrass and tall fescue, while St. Augustinegrass and bahairgrass did not exhibit the PIB.

Atmosphere. Cowling and Koziol (14) found perennial ryegrass exposed to two levels of SO₂ (50 and 400 µg m⁻³) to show visible injury symptoms, but no significant decrease in

net photosynthesis was observed. However, Beard (5) reported that the destruction of chlorophyll by SO₂ results in the inhibition of photosynthesis. Ho and Trappe (28) reported that the intensity of mycorrhiza formation in forage grasses relates directly to photosynthetic activity or assimilate availability, and when tall fescue was exposed to 0.1 ppm ozone for 3 months the reduction in the intensity of mycorrhiza formation was possibly caused by reduced photosynthesis in the host.

Wind. Grace and Thompson (23) found tall fescue plants subjected to simulated wind conditions in a controlled environment wind tunnel to have reduced rates of photosynthesis, higher mesophyll resistance and lower leaf surface resistance than control plants. The high mesophyll resistance in the wind-treated plant was attributed to reduced water content. However, Russel and Grace (59) found no difference in the gross photosynthesis of tall fescue or perennial ryegrass when subjected to wind speeds of 7.4 m s⁻¹ or 1.0 m s⁻¹.

CULTURAL EFFECTS

Mineral Nutrition. Hull (29) reported that a Merion Kentucky bluegrass turf fixed more ¹⁴CO₂ at high fertility rates (24-4-8 or 48-8-16 g m⁻² N-P-K) than at low fertility (12-2-4 g m⁻² N-P-K). Davidson and Robson (15) found perennial ryegrass plants grown in a solution culture high in N (220 μg g⁻¹) to have canopy photosynthetic rates (g CO₂ m⁻² h⁻¹) 30% higher than plants grown in low N (40 μg g⁻¹).

Tall fescue and creeping bentgrass, under growth conditions in Virginia, showed increased photosynthesis, on a plot area basis, for high N treatments (55). High N fertility levels have been shown to increase net photosynthesis, on a dry weight basis, for Tifgreen bermudagrass (61) and Cohansey bentgrass (62). In centipedegrass (*Eremochloa ophiuroides* (Munro.) Hack.) Walker and Ward (68) found increasing N fertility to increase CER on a leaf area basis, while increasing K fertility decreased CER. Robson and Parsons (56) found an increase in the photosynthetic rate, on both a leaf area and canopy basis, of perennial ryegrass at high N fertility levels. A comparison of the observed rates of canopy photosynthesis with those predicted by a mathematical model of canopy photosynthesis indicated that it was the effect of N on single leaf photosynthesis, rather than differences between the communities in leaf area which led to the observed differences in photosynthesis. Ruetz (58) found fertilized red fescue to have higher CER (leaf dry weight or leaf area basis) than unfertilized and that during the growing season the unfertilized plants had a continual decline in CER. Mehall et al. (43) found no relationship between CER and Kentucky bluegrass tissue K or P concentrations. In a growth chamber simulation of a late summer through mid fall Virginia growth cycle, Schmidt and Snyder (63) found applications of FeDTPA to decrease net photosynthesis of Pennncross creeping bentgrass. Hull (30) found that diurnal photosynthate partitioning was

independent of fertility level in Kentucky bluegrass. However, translocation of assimilates from leaves to stems was faster in heavily fertilized turf (48-8-16 g m⁻² N-P-K) while roots received more photosynthate in low fertility (12-2-4 g m⁻² N-P-K) turf. Fertility influences were most evident during midsummer when roots and rhizomes constituted stronger sinks for assimilates.

Mowing/Clipping. Krans and Beard (37) reported that rates of apparent photosynthesis based on unit leaf area were higher in Merion Kentucky bluegrass plants clipped semiweekly than biweekly, but when based on total leaf area per pot this response was reversed. Youngner et al. (83) attributed the greater tolerance to mowing of Merion Kentucky bluegrass to higher leaf sheath CER in this variety. Ollerenshaw and Incoll (49) found that the photosynthetic rates of leaves of annual and perennial ryegrass were higher in swards cut constantly at 3 cm when compared to plants clipped at 9 cm and that the photosynthetic rate of annual ryegrass was higher than perennial ryegrass soon after mowing but the perennial ryegrass leaves quickly adapted to the higher irradiances received after clipping. In forage bermudagrass Morgan and Brown (46) found much lower CER for stands clipped weekly compared to plots mowed monthly, which was attributed to the lower LAI in the weekly mowed plots. Alexander and McCloud (3) found severe clipping treatments, where large amounts of leaf and stem tissue were removed, to

significantly reduce photosynthesis (on a leaf area basis) in bermudagrass and attributed the reduction to lack of leaf greenage in the stubble after clipping. Hart and Lee (25) reported that the much higher rate of NCE in younger leaves may explain the high production of frequently cut Coastal bermudagrass stands. As was reported in the Light section of this paper Dienum (16) demonstrated that defoliation and shading of the axillary tillers of vegetative annual and ryegrass plants stimulated leaf photosynthesis of the main shoot. Gifford and Marshall (21) reported that CER of the main shoot leaves of annual ryegrass were 15% greater the day after tiller defoliation than just before defoliation, which was attributed to a measured lower gas-phase resistance in the defoliated plants. Clark et al. (11) found that the photosynthetic rate of excised annual ryegrass leaves began to decline rapidly 1-2 min. after excision with two breaks of slope at 15 and 30 min. Examination of stomata found complete optical closure at 15 min. after excision.

Chemical. Kaufmann and Williamson (36) tested several chemicals to manipulate water consumption in Merion Kentucky bluegrass and measured the effect of these chemicals on photosynthesis. The wetting agent Hydrowet and the fungicide benomyl (Methyl-1-(butylcarbamoyl)-2-benzimidazole-carbamate) significantly reduced CER while Aquagro (wetting agent) and the fungicide iprodione (3-(3,5-Dichlorophenyl)-N-(1-methylethyl)-2,4-dioxo-1-

imidazolidinecarboxamide) did not affect photosynthesis. DeMur et al. (17) reported that siduron (1-(2-methylcyclohexyl)-3-phenylurea) inhibited electron transport in isolated chloroplasts of bermudagrass and Kentucky bluegrass with the site of inhibition in photosystem II between water splitting and photosystem I. Moss (45) found a high correlation between grasses with a high photosynthetic activity and atrazine tolerance. Bromacil (5-bromo-3-*sec*-butyl-6-methyluracil) has been shown to inhibit photosynthesis in Kentucky bluegrass (65,66). Yang and Bingham (82) found metribuzin (4-amino-6-*tert*-butyl-3-(methylthio)-*as*-triazin-5(4*H*)-one) to inhibit the CO₂ uptake of six cultivars of bermudagrass, but full photosynthetic rate was recovered within 24 h after treatment for low metribuzin rates and several days after treatment for high metribuzin rates. Karnok and Beard (35) found exogenous applications of gibberellic acid to increase the daytime CER of two cultivars of bermudagrass (Ormond and Pee Dee) and decrease daytime CER in Floratam St. Augustinegrass, after growth at chilling temperatures.

Irrigation/Water Stress. Schmidt and Snyder (63) found net photosynthesis to decline with decreasing moisture levels in Penncross creeping bentgrass. Asay et al. (4) reported rates of net photosynthesis in tall fescue to be significantly higher under irrigated vs. non-irrigated conditions. Brown and Simmons (8) subjected the roots of tall fescue to drying conditions to induce water stress and

reported a decrease in net photosynthesis which was associated with decreases in stomatal plus boundary layer conductance and mesophyll conductance. Agnew and Carrow (1) found that after a water stress irrigation treatment (irrigation at -0.400 MPa for 99 days) stomatal diffusive resistance (R_s) increased in Kentucky bluegrass and concluded that this increase in R_s would decrease photosynthetic rate. Woledge and Parsons (81) reported a decrease in gross canopy photosynthesis in perennial ryegrass when measured at low humidity. Wilson (72) found perennial ryegrass selection lines with high calculated R_s maintained leaf photosynthetic rates longer than selection lines with low R_s when deprived of water. Jones et al. (33) reported that, after water stress, the canopy photosynthesis of both simulated and field-grown perennial ryegrass was significantly reduced. In the field grown plants the reduction was partially due to a lower leaf area but the rate of leaf photosynthesis (P_{max} / LAI) was reduced by about 40% which was attributed to a measured increase in stomatal resistance. In perennial ryegrass, Sheehy et al. (64) found an increase in leaf resistance to gas exchange with increasing moisture stress, with a corresponding increase in CO_2 compensation point and a decrease in leaf and canopy photosynthesis. Peacock and Dudeck (54) investigated the effect of irrigation scheduling on the CER of St. Augustinegrass and found that irrigation at 6 day

intervals reduced the CER prior to irrigation, but the CER returned to normal levels soon after irrigation.

Compaction. Agnew and Carrow (1) reported that long term compaction (compaction treatments equivalent to 720 J energy over a 99-day period) increased R_s in Kentucky bluegrass and concluded that higher R_s would result in lower photosynthesis. On zoysiagrass in Japan, Akiyama and Kubo (2) reported a maximum depression in photosynthesis four days after application of compression treatments (0.00, 2.50, 3.75, and 5.00 kg cm⁻²) but the plants compressed at 2.5 kg cm⁻² recovered their photosynthetic rate comparable to control plants within 3 weeks after compression, while the plants compressed to 5.00 kg cm⁻² recovered 70% of the control plot photosynthesis within three weeks.

PHYSIOLOGICAL, MORPHOLOGICAL and GENETIC EFFECTS

Genetics. Watschke et al. (70) measured significantly different rates of CER among ten strains of Kentucky bluegrass, but the strains did not differ in their CO₂ compensation points. Asay et al. (4) reported significant differences for net carbon exchange (NCE) among tall fescue clonal lines and their polycross progenies under sward conditions in the field, with heritability estimates from 0.57-0.83, indicating that genetic progress could be made through selection for NCE rate in tall fescue. Cohen et al. (12) also found genetic variability among tall fescue for NCE with low yielding selections exhibiting significantly higher NCE than higher yielding selections. The authors

concluded that single-leaf NCE is a necessary component of forage yield, but is apparently not a major component for yield determination. Youngner et al. (83) showed significant differences between Merion (higher CER) and Newport Kentucky bluegrass for net assimilation on a whole plant basis but not when expressed on an individual leaf basis. The higher rate for Merion was attributed to a higher rate of CER for the leaf sheath in Merion. Joseph et al. (34) found that net photosynthesis on a leaf area and leaf weight basis increased significantly with ploidy in a 4X, 6X, 8X, and 10X allopolyploid series of tall fescue. Krueger and Miles (40) found the electron transport activity for Photosystem I to be higher in a decaploid tall fescue as compared to a common hexaploid genotype. The decaploid genotype also exhibited a higher photosystem whole chain (Photosystem II plus Photosystem I uncoupled) activity, suggesting a connection between polyploidy and increased electron transport activity. Cooper and Wilson (13) found populations and genotypes of annual and perennial ryegrass to differ in their photosynthetic rate at both high and low light intensity with roughly equal heritabilities under both conditions. The data suggested that effective response to selection should be possible for both light-saturated and light-limited photosynthesis.

Leaf Age/Position. Hart and Lee (24) found the NCE of bermudagrass leaves to be highest at collar emergence and decrease with age. Jewiss and Woledge (32) found the

apparent photosynthesis of tall fescue leaves to decline in a curvi-linear fashion when measured from full expansion to leaf death. Woledge and Leafe (80) found that canopy photosynthesis of perennial ryegrass declined due to leaf age when no further leaves were produced after flowering. The dry weight of the leaf did not change as it aged and net photosynthesis results were similar when expressed on either a leaf area or dry weight basis. Photosynthesis in leaves of bahiagrass is relatively stable from emergence to 30 days after emergence, than exhibits a severe decline starting 45 days after emergence (60). Krans and Beard (38) measured the net photosynthesis of seedlings of Kentucky bluegrass and red fescue from seedling emergence to 10 weeks after emergence. Net photosynthesis was greatest one week after emergence for both species. Wilson and Cooper (73) found apparent photosynthesis in fully expanded perennial ryegrass leaves to be higher in in the lower (older) leaves than in the upper (younger) leaves and for any particular leaf, maximum photosynthesis was attained prior to full expansion. Silcock and Wilson (67) measured photosynthesis in fescues which differed in leaf orientation and reported differences in the photosynthesis/ transpiration ratio based on leaf orientation.

Electron Transport. Chen et al. (10) measured the photosynthetic activity of isolated chloroplasts of bermudagrass and concluded that the high activity of bermudagrass could be supported by the photophosphorylation

capacities measured in these chloroplast studies. As was discussed in the Genetics section Krueger and Miles (40) suggested a connection between ploidy and increased electron transport activity. In further studies on electron transport in decaploid tall fescue Krueger et al. (41) found the decaploid tall fescue to have a higher plastocyanin content than the hexaploid type. Isolated thylakoid antibodies did not inhibit electron transport (diaminodiurene to methyl viologen) strengthening the hypothesis of plastocyanin as an internal electron shuttle.

Inflorescence Assimilation. The inflorescence of annual bluegrass has been shown to be an important assimilatory organ after grain ripening when it exports more than 50% of its assimilate to the stem, roots and other tillers (52). Ong et al. (51) investigated the assimilation of $^{14}\text{CO}_2$ by the inflorescence of annual bluegrass and perennial ryegrass determined from inflorescence emergence to seed shedding. Both species exhibited the same fixation pattern, with the inflorescence being the greatest assimilatory organ on the reproductive tiller. Except for the seeds all parts of the inflorescence showed significant assimilatory activity with the lemma and palea accounting for 40-50% of ^{14}C fixed.

Feedback Inhibition. In annual ryegrass Hansen (25) found that on the first day of a period of high irradiance, CO_2 assimilation was higher on a leaf area basis than on the following day of high irradiance, and an accumulation of storage material took place. On the first day of a period

of low irradiance, the assimilation was lower than on the following a day of low irradiance, and there was a depletion in stored assimilates. These effects were most evident during a regrowth period, indicating a change in metabolic sink demand. Hansen (25) proposed that a strong feedback mechanism between sources and sinks exists, in the sense that accumulation of products will inhibit assimilation.

REFERENCES

- 1) Agnew, M.L. and R.N. Carrow. 1985. Soil compaction and moisture stress preconditioning in Kentucky bluegrass. II. Stomatal resistance, leaf water potential, and canopy temperature. *Agron. J.* 77:878-884.
- 2) Akiyama, T. and S. Kubo. 1978. Treading on the grasslands. Photosynthesis and dry matter production of native grasses. *Bull. Natl. Grassl. Res. Inst.* 12:23-31.
- 3) Alexander, C.W. and D.E. McCloud. 1962. CO₂ uptake (net photosynthesis) as influenced by light intensity of isolated bermudagrass leaves contrasted to that of swards under various clipping regimes. *Crop Sci.* 2:132-135.
- 4) Asay, K.H., C.J. Nelson, and G.L. Horst. 1974. Genetic variability for net photosynthesis in tall fescue. *Crop. Sci.* 14:571-574.
- 5) Beard, J.B. 1973. *Turfgrass: Science and culture.* Prentice-Hall, Inc. Englewood Cliffs, NJ.
- 6) Brown, R.H. and W.V. Brown. 1975. Photosynthetic characteristics of *Panicum milioides*, a species with reduced photorespiration. *Crop Sci.* 15:681-685.
- 7) ----- and V.E. Gracen. 1972. Distribution of the postillumination CO₂ burst among grasses. *Crop Sci.* 12:30-33.
- 8) ----- and R.E. Simmons. 1979. Photosynthesis of grass species differing in CO₂ fixation pathways. I. Water use efficiency. *Crop Sci.* 19:375-379.
- 9) Burian K. and C. Winter. 1976. Effect of different day-length on photosynthesis of grasses. *Photosynthetica.* 10:25-32.
- 10) Chen, T.M., R.H. Brown and C.C. Black. 1968. Photosynthetic activity of chloroplasts isolated from bermudagrass (*Cynodon dactylon*) a species with high photosynthetic capacity. *Plant Physiol.* 44:649-654.
- 11) Clark, B.J., J.L. Prioul, and H. Couderc. 1977. The physiological response to cutting in Italian ryegrass. *J. British Grassl. Soc.* 32:1-5.
- 12) Cohen, C.J., D.O. Chilcote, and R.V. Frakes. 1982. Gas exchange and leaf area characteristics of four tall fescue selections differing in forage yield. *Crop Sci.* 22:709-711.

- 13) Cooper, J.P. and D. Wilson. 1970. Variation in photosynthetic rate in *Lolium*. Proc. Int. Grassl. Congress. 11:522-527.
- 14) Cowling, D.W. and M.J. Koziol. 1978. Growth of ryegrass (*Lolium perenne* L.) Exposed to SO₂. I. Effects on photosynthesis and respiration. J. Exp. Bot. 29:1029-1036.
- 15) Davidson, I.A. and M.J. Robson. 1986. Effect of temperature and nitrogen supply on the growth of perennial ryegrass and white clover. 2. A comparison of monocultures and mixed swards. Annals of Bot. 57:709-719.
- 16) Deinum, B. 1976. Photosynthesis and sink size: An explanation for the low productivity of grass swards in autumn. Neth. J. Agric. Sci. 24:238-246.
- 17) DeMur, A.R., J.A. Swader, and V.B. Youngner. 1972. Siduron inhibition of photosystem II in isolated chloroplasts. Pest. Biochem Phys. 2:337-341.
- 18) Downes, R.W. and J.D. Hesketh. 1968. Enhanced photosynthesis at low oxygen concentrations: Differential response of temperate and tropical grasses. Planta (Berl.). 78:79-84
- 19) Downton, W.J.S. and E.B. Tregunna. 1968. Carbon dioxide compensation-its relation to photosynthetic carboxylation reactions, systematics of the Gramineae, and leaf anatomy. Can J. Bot. 46:207-215.
- 20) Duff, D.T. and J.B. Beard. 1974. Supraoptimal temperature effects upon *Agrostis palustris*. Part II. Influence on carbohydrate levels, photosynthetic rate, and respiration rate. Physiol. Plant. 32:18-22.
- 21) Gifford, R.M. and C. Marshall. 1973. Photosynthesis and assimilate distribution in *Lolium multiflorum* Lam. following differential tiller defoliation. Aust. J. of Biol. Sci. 26:517-526.
- 22) Glacoleva, T.A. and O.V. Zalensky. 1978. Oxygen effects on photosynthesis and ¹⁴C metabolism in desert plants. Plant Physiol. 62:204-209.
- 23) Grace, J. and J.R. Thompson. 1973. The after-effect of wind on the photosynthesis and transpiration of *Festuca arundinacea*. Physiol. Plant. 28:541-547.
- 24) Hart, R.H. and D.R. Lee. 1971. Age vs. net CO₂ exchange rate of leaves of Coastal bermudagrass. Crop Sci. 11:598-599.

- 25) Hansen, G.K. 1978. Utilization of photosynthates for growth respiration, and storage in tops and roots of *Lolium multiflorum*. *Physiol. Plant.* 42:5-13.
- 26)----- . 1977. Adaptation to photosynthesis and diurnal oscillation of root respiration rates for *Lolium multiflorum*. *Physiol. Plant.* 39:275-279.
- 27) Hay, R.K.M. and O.M. Heide. 1983. Specific photoperiod stimulation of dry matter production in a high-latitude cultivar of *Poa pratensis*. *Physiol. Plant.* 57:135-142.
- 28) Ho, I. and J.M. Trappe. 1984. Effects of ozone exposure on mycorrhiza formation and growth of *Festuca arundinacea*. *Environ. Exp. Bot.* 24:71-74.
- 29) Hull, R.J. 1976. A carbon-14 technique for measuring photo synthate distribution in field grown turf. *Agron. J.* 68:99- 102.
- 30)----- . 1981. Diurnal variation in photosynthate partitioning in Kentucky bluegrass turf. *Proc. Int. Turf. Res. Conf.* 4:509-517
- 31) Imai, H., M. Fukuyama and T. Harada. 1973. Comparative studies on the photosynthesis of higher plants. III. Differences in response to various factors affecting the photosynthetic rate between C-4 and C-3 plants. *Soil Sci. Plant Nutr.* 19:61-71.
- 32) Jewiss, O.R. and J. Woledge. 1967. The effect of age on the rate of apparent photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). *Annals of Bot.* 31:661-671.
- 33) Jones, M.B., E.L. Leafe and W. Stiles. 1980. Water stress in field-grown perennial ryegrass. I. Its effect on growth, canopy photosynthesis and transpiration. *Ann. Appl. Biol.* 96:87-101.
- 34) Joseph, M.C., D.D. Randell and C.J. Nelson. 1981. Photosynthesis in polyploid tall fescue. II. Photosynthesis and ribulose-1,5-bisphosphate carboxylase of polyploid tall fescue. *Plant Physiol.* 68:894-898.
- 35) Karnok, K.J. and J.B. Beard. 1983. Effects of gibberellic acid on the CO₂ exchange rates of bermudagrass and St. Augustinegrass when exposed to chilling temperatures. *Crop Sci.* 23:514-517.
- 36) Kaufman, J.E. and D.R. Williamson. 1981. Chemical manipulation of stomatal number and behavior in Merion Kentucky bluegrass (*Poa pratensis* L.) *Proc. Int. Turf. Res. Conf.* 4:501-516.

- 37) Krans, J.V. and J.B. Beard. 1985. Effects of clipping on growth and physiology of 'Merion' Kentucky bluegrass. *Crop Sci.* 25:17-20.
- 38) ----- and ----- . 1977. The effects of stage of development on selected physiological and morphology parameters in Kentucky bluegrass and red fescue. *Proc. Int. Turf. Res. Conf.* 3:89-95.
- 39) Krenzer, E.G. and D.N. Moss. 1969. Carbon dioxide compensation in grasses. *Crop Sci.* 9:619-621.
- 40) Krueger, R. W. and D. Miles. 1981. Photosynthesis in fescue. III. Rates of electron transport in a polyploid series of tall fescue plants. *Plant Physiol.* 68:1110-1114.
- 41) -----, D.D. Randall and D. Miles. 1984. Photosynthesis in tall fescue. V. Analysis of high PSI activity in a decaploid genotype. *Plant Physiol.* 76:903-909.
- 42) Labhart, C., J. Nosberger and C.J. Nelson. 1983. Photosynthesis and degree of polymerization of fructan during reproductive growth of meadow fescue at two temperatures and two photon flux densities. *J. Exp. Bot.* 34:1037-1046.
- 43) Mehall, B.J., R.J. Hull, and C.R. Skogley. 1984. Turf quality of Kentucky bluegrass cultivars and energy relations. *Agron. J.* 76:47-50.
- 44) Miller, V.J. 1960. Temperature effect on the rate of apparent photosynthesis of Seaside bent and bermudagrass. *Am. Soc. Hort. Sci.* 75:700-703.
- 45) Moss, D.N. 1968. Relation in grasses of high photosynthetic capacity and tolerance to atrazine. *Crop Sci.* 8:774.
- 46) Morgan, J.A. and R.H. Brown. 1983. Photosynthesis and growth of bermudagrass swards. I. Carbon dioxide exchange characteristics of swards mowed at weekly and monthly intervals. *Crop Sci.* 23:347-352.
- 47) Murata, Y. and J. Iyama. 1963. Studies on the photosynthesis of forage crops. I. Diurnal changes in the photosynthesis of several grasses and barley seedlings under constant temperature and light intensity. *Proc. Crop Sci. Soc. Japan.* 31:311-314.

- 48)-----and----- . 1963. Studies on the photosynthesis of forage crops. II. Influence of air-temperature upon the photosynthesis of some forage and grain crops. Proc. Crop Sci. Soc. Japan. 31:315-321.
- 49)Ollerenshaw, J.H. and L.D. Incoll. 1979. Leaf photosynthesis in pure swards of two grasses (*Lolium perenne* and *Lolium multiflorum*) subjected to contrasting intensities of defoliation. Ann. Appl. Biol. 92:133-142.
- 50)-----, W.S. Stewart, J. Gallimore and R.H. Baker. 1986. Low-temperature growth in grasses from northern latitudes. J. Agric. Sci. 87:237-239.
- 51)Ong, C.K., K.E. Colvill and C. Marshall. 1978. Assimilation of $^{14}\text{CO}_2$ by the inflorescence of *Poa annua* L. and *Lolium perenne* L. Ann. Bot. 42:855-862.
- 52)----- and C. Marshall. 1975. Assimilate distribution in *Poa annua* L. Ann. Bot. 39:413-421.
- 53)Pammentor, N.W., P.M. Drennan and V.R. Smith. 1986. Physiological and anatomical aspects of photosynthesis of two *Agrostis* species at a sub-antarctic island. New Phytol. 102:143-160.
- 54)Peacock, C.H. and A.E. Dudeck. 1984. Physiological response of St. Augustinegrass to irrigation scheduling. Agron. J. 76:275-279.
- 55)Powell, A.J., R.E. Blaser and R.E. Schmidt. 1967. Physiological and color aspects of turfgrass with fall and winter nitrogen. Agron. J. 59:303-307
- 56)Robson, M.J. and A.J. Parsons. 1978. Nitrogen deficiency in small closed communities of S24 ryegrass. I. Photosynthesis respiration, dry matter production and partition. Ann. Bot. 42:1185-1197.
- 57)Rogers, R.A., J.H. Dunn and C.J. Nelson. 1977. Photosynthesis and cold hardening in zoysia and bermudagrass. Crop Sci. 17:727-732.
- 58)Ruetz, W.F. 1973. The seasonal pattern of CO_2 exchange of *Festuca rubra* L. in a montane meadow community in northern Germany. Oecologia (Berl.) 13:247-269.
- 59)Russel, G. and J. Grace. 1978. The effect of wind on grasses. J. Exp. Bot. 29:1249-1258.
- 60)Sampaio, E.V.S.B., E.R. Beaty and D.A. Ashley. 1976. Bahiagrass regrowth and physiological aging. J. Rng. Manage. 29:316-319.

- 61) Schmidt, R.E. and R.E. Blaser. 1969. Effect of temperature, light, and nitrogen on growth and metabolism of 'Tifgreen' bermudagrass (*Cynodon* spp.) Crop Sci. 9:5-9.
- 62)----- and ----- . 1967. Effect of temperature, light, and nitrogen on growth and metabolism of 'Cohansey' bentgrass (*Agrostis palustris* Huds.) Crop Sci. 7:447-451.
- 63)----- and V. Snyder. 1984. Effects of N, temperature, and moisture stress on the growth and physiology of creeping bentgrass and response to chelated iron. Agron. J. 76:590-594.
- 64)Sheehy, J.E., R.M. Green and M.J. Robson. 1975. The influence of water stress on the photosynthesis of a simulated sward of perennial ryegrass. Ann. Bot. 39:387-401.
- 65)Shriver, J.W. and S.W. Bingham. 1973. Selectivity of bromacil on Kentucky bluegrass and orchard grass. Crop Sci. 13:45-49.
- 66)----- and ----- . 1973. Physiological effects of bromacil on Kentucky bluegrass and orchardgrass. Weed Sci. 21:212-216.
- 67)Silcock, R.G. and D. Wilson. 1982. The effects of leaf orientatation on photosynthesis, transpiration, and diffusive conductance of leaves of contrasting *Festuca* species. New Phytol. 90:27-36.
- 68)Walker, R.H. and C.Y. Ward. 1974. Influence of N and K nutrition on net photosynthesis, dark respiration, and carbohydrates in centipedegrass. Proc. Int. Turf. Res. Conf. 2:196-209.
- 69)Watschke, T.L., R.E. Schmidt, E.W. Carson and R.E. Blaser. 1973. Temperature influence on the physiology of selected cool season turfgrasses and bermudagrass. Agron. J. 65:591 -594
- 70)-----,-----,----- and ----- . 1972. Some metabolic phenomena of Kentucky bluegrass under high temperature. Crop Sci. 12:87-90.
- 71)Wilkinson, J.F., J.B. Beard and J.V. Krans. 1985. Photosynthetic-respiratory responses of 'Merion' Kentucky bluegrass and 'Pennlawn' red fescue at reduced light intensities. Crop Sci. 15:165-168.

- 72) Wilson, D. 1975. Leaf growth, stomatal diffusion resistances and photosynthesis during droughting of *Lolium perenne* populations selected for contrasting stomatal length and frequency. *Ann. Appl. Biol.* 79:67-82.
- 73)----- and J.P. Cooper. 1969. Apparent photosynthesis and leaf characters in relation to leaf position and age, among contrasting *Lolium* genotypes. *New Phytol.* 68:645-655.
- 74) Winstead, C.W. and C.Y. Ward. 1974. Persistence of southern turfgrasses in a shade environment. *Proc. Int. Turf. Res. Conf.* 2:221-230.
- 75) Woledge, J. 1979. Effect of flowering on the photosynthetic capacity of ryegrass leaves grown with or without natural shading. *Ann. Bot.* 44:197-207.
- 76)----- . 1978. The effect of shading during vegetative and reproductive growth on the photosynthetic capacity of leaves in a grass swards. *Ann. Bot.* 42:1085-1089.
- 77)----- . 1977. The effects of shading and cutting treatments on the photosynthetic rate of ryegrass leaves. *Ann. Bot.* 41:1279-1286.
- 78)----- and W.D. Dennis. 1982. The effect of temperature on photosynthesis of ryegrass on white clover leaves. *Ann. Bot.* 50:25-35.
- 79)----- and O.R. Jewiss. 1969. The effect of temperature during growth on the subsequent rate of photosynthesis in leaves of tall fescue (*Festuca arundinacea* Schreb.). *Ann. Bot.* 33:897-913.
- 80)----- and E.L. Leafe. 1976. Single leaf and canopy photosynthesis in a ryegrass swards. *Ann. Bot.* 40:773-783.
- 81)----- and A.J. Parsons. 1986. The effect of temperature on the photosynthesis of ryegrass canopies. *Ann. Bot.* 57:487-497.
- 82) Yang, Y. and S.W. Bingham. 1984. Effects of metribuzin on net photosynthesis of goosegrass (*Eleusine indica*) and bermudagrass (*Cynodon* spp.). *Weed Sci.* 32:247-250.
- 83) Youngner, V.B., F. Nudge and R. Ackerson. 1976. Growth of Kentucky bluegrass leaves and tillers with and without defoliation. *Crop Sci.* 16:110-113.