

Comparative Ecophysiology of Green Foxtail
(Setaria viridis (L.) Beauv.) and Spring Wheat

by

Brian John Douglas

A thesis
presented to the University of Manitoba
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy
in
Plant Science

Winnipeg, Manitoba

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ISBN 0-315-44129-1

COMPARATIVE ECOPHYSIOLOGY OF GREEN FOXTAIL
(SETARIA VIRIDIS (L.) BEAUV.) AND SPRING WHEAT

BY

BRIAN JOHN DOUGLAS

A thesis submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
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DOCTOR OF PHILOSOPHY

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" pluralitas non est ponenda sine necessitate "

(" multiplicity ought not to be posited without necessity ")

" Ockham's razor " - William of Ockham 1280-1349

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ABSTRACT

Douglas, Brian John. Ph.D. The University of Manitoba, November, 1987.
Comparative ecophysiology of green foxtail (*Setaria viridis* (L.) Beauv.)
and spring wheat. Major Professor; Ian N. Morrison.

The growth and development of green foxtail and spring wheat (cv. Benito) were studied in outdoor rain-out shelters filled with clay loam soil, in 1984 and 1985. Foxtail and wheat were established at 400 and 200 plants m^{-2} , respectively, in late May, and approximately 21 days after emergence two irrigation schemes were imposed (25 and 5 mm $week^{-1}$) to represent wet and dry situations. Plant development was assessed at weekly intervals. In both years, at all harvests, wheat was taller, and had a greater leaf area, leaf weight and total biomass than foxtail. Water stress significantly reduced the growth of both species. The leaf area ratio and specific leaf area of foxtail increased in response to shading by the wheat canopy. Water stress caused a significant reduction in seed yield of both species. In both years wheat was more competitive than foxtail as a result of environmental conditions favoring the growth of wheat over that of foxtail.

Controlled environment studies were conducted to elucidate the relative importance of temperature and water stress on the growth and competitive ability of the two species. Foxtail and wheat were grown singly and in combination at 30/25 C and 20/15 C in both water stressed and unstressed conditions. Foxtail had higher relative growth rates based on total biomass, leaf area, leaf weight and stem weight and a

greater extent of development in these parameters than did wheat. At 20/15 C wheat was superior to foxtail in these same attributes. Within a given temperature regime water deficit had a significant effect, but the effect was small compared to that of temperature. Foxtail effectively suppressed wheat at 30/25 C, while wheat suppressed the foxtail at 20/15 C.

The water relations of foxtail and wheat seedlings were studied, in a controlled environment at 25/20 C, in drying soil, to assess the physiological responses to soil water deficit. Foxtail maintained a higher water potential than did wheat, but this was attained at a lower relative water content.

However there was no evidence to support the contention that the C₄ photosynthetic pathway is an adaptation to dry environments, or that it is of competitive advantage in such environments. When foxtail and wheat were examined in their respective ecological niches there was no evidence for a superior competitive ability for foxtail in water limited environments.

ACKNOWLEDGEMENTS

I would like to express my appreciation to the following:

Drs. I.N. Morrison, R.D. Hill. and G.C. Racz for acting as committee members.

the Statistical Advisory Service, University of Manitoba for assistance with the data analysis.

the University of Manitoba for providing financial support in the form of a Graduate Studies Fellowship.

Dr. C.J.T. Spitters, Department of Theoretical Production Ecology, Agricultural University, Wageningen, The Netherlands, for supplying copies of unpublished manuscripts and for providing helpful suggestions on methodology.

the numerous graduate and summer students who aided with the outdoor work.

and finally my wife Catherine for her patience, tolerance and moral support.

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INTRODUCTION

Green foxtail (Setaria viridis (L.) Beauv) is an annual grassy weed with the C₄ photosynthetic carbon reduction cycle (PCRC). The C₄ system has often been proposed to confer a competitive advantage to weed species particularly under hot, arid climatic conditions (Chen et al. 1970; Black 1971) . On a worldwide basis 32 of the 76 worst weeds are C₄ species (Holm et al. 1977). However the superiority of C₄ over C₃ plants decreases as the level of organization progresses from cellular events to whole plant growth. The PCRC of a plant is but a single component of an integrated system and the advantages of the C₄ system in terms of weed-crop competition have been more closely examined in recent years (Cohen 1970 ; Baskin and Baskin 1978 ; Patterson 1985).

Green foxtail is currently one of the most abundant and widespread weed species in western Canada (Thomas and Wise 1984) where plant growth is limited primarily by a lack of precipitation (Oosterveld and Nicholaichuk 1983). Many C₄ weeds are proposed to be adapted to, and competitive in semiarid to arid environments (Black 1971 ; Jordan and Shaner 1979) and as green foxtail is most prevalent in western Canada (Alex et al. 1972), the C₄ PCRC may be advantageous in competitive situations. Field studies have shown that the competitive effects of green foxtail in cereals (Sturko 1978 ; Blackshaw et al. 1981b), corn (Nieto and Staniforth 1961 ; Sibuga Bandeen 1980a,b), and soybeans (Staniforth 1965) varies with environmental conditions, particularly temperature and precipitation. Also, Sturko (1978) reported that green

foxtail was more competitive in a semidwarf wheat than in a standard height wheat, which indicates that shading is very important in the interaction between the two species.

Computer simulation models have demonstrated that temperature, water potential, radiation, and dry weight accumulation are determining factors in the growth of Setaria spp. and their subsequent competitive ability at any given growth stage (Orwick et al. 1978). The sensitivity of foxtail growth to environmental factors is evident from the inconsistency in results of field studies (Blackshaw et al. 1981b). Although several studies have examined the comparative growth of foxtails in isolation, there are few detailed reports of the comparative crop-foxtail growth in a competitive situation. A summary of the biology and ecology of green foxtail is presented in Douglas et al. (1985).

Studies on the variability in deleterious effects of weeds, as determined by environmental conditions are important in that they aid in refining the concept of an economic threshold, above which weed control practices could be profitable. The potential effects of weeds such as wild oats (Avena fatua L.) on crop yield can be more accurately predicted, than for green foxtail, on the basis of density and time of emergence (Dew 1972), as they have a greater degree of niche overlap with cereals than does green foxtail (Barrett 1983). In contrast the growth and competitive ability of green foxtail is more environmentally sensitive than the growth of wild oats, and this, coupled with a potentially large degree of temporal niche separation, necessitates that environmental conditions must be taken into account in attempting to assess the competitive effects of green foxtail in cereals.

The purpose of this study was to examine the primary environmental factors which influence the growth and competitive ability of green foxtail in spring wheat in relation to the intrinsic differences in ecophysiology of the two species.

LITERATURE REVIEW

INTRODUCTION

In studying the comparative ecophysiology of green foxtail and wheat a distinction must be made between plant characters which are beneficial to survival and reproduction, and those which determine the relative competitive ability of the two species. "It is important to recognize that the ability to survive stress and the ability to outcompete a neighbor or control a resource within a distinct area are not necessarily the same phenomena" (Radosevich and Holt 1984). While not mutually exclusive, a species which is competitive in a seral situation may utilize a different strategy than one that is competitive in a climax plant community (Barbour et al. 1980).

Green foxtail is primarily a weed of cultivated fields, which represent seral communities, and from an agricultural viewpoint we are most interested in the detrimental effects of weeds on crop yield. The following literature review will thus concentrate on the comparative physiology of green foxtail and wheat in relation to competition, rather than to survival and reproduction.

The field of soil-plant-atmosphere water relations has been extensively studied and interested readers are referred the books by Kramer (1983a), Turner and Jones (1980), and Taylor (1983); the series of volumes edited by Kozlowski entitled "Water Deficits and Plant Growth"; and review articles by Boyer and McPherson (1975), Begg and Turner

(1976), Hsiao (1973) , Hanson and Hitz (1982) and Boyer (1985). In the present review the relevant features of plant water relations as they relate to crop-weed competition and plant ecology will be considered but a detailed and comprehensive review of the literature on plant water relations is not attempted. " The field is wide and to cover it is not only beyond my capacity but would provide a thin and insipid spread " (Weatherley 1970).

A list of abbreviations, symbols and dimensions, where appropriate, for parameters mentioned in the text, is included in Appendix Table 1.

GENERAL ECOPHYSIOLOGY OF C₃ AND C₄ SPECIES

As green foxtail is a C₄ species and wheat is a C₃ species a general understanding of the comparative physiology and ecology of these groups is necessary before their competitive abilities in a given environment can be assessed.

Carbon fixation

The C₄ PCRC acts primarily as a mechanism to concentrate CO₂ within the vascular bundle of the leaf. This effectively favors the carboxylase function of RuBP carboxylase:oxygenase (RuBP-C:O) over the oxygenase function and eliminates any effect due to the photosynthetic carbon oxidation cycle (PCOC). C₃ species lack this CO₂ concentrating mechanism and thus under atmospheric oxygen levels (21%) have reduced photosynthetic efficiency due to the PCOC (Leopold and Kriedemann 1975). This reduction can be 12 to 20% at 10 C and 45 to 60% at 40 C (Long 1983). The enzyme responsible for the initial CO₂ fixation step in C₄

species, PEP carboxylase, also has a higher affinity (lower K_m) for CO_2 , than does RuBP-C:O, so that net photosynthesis in C_4 species becomes CO_2 saturated at a much lower intercellular CO_2 concentration (c_i). At a given atmospheric CO_2 concentration (c_a) the gradient in CO_2 levels between the air surrounding the leaf and the internal leaf surface (ΔCO_2) will be greater for C_4 species than C_3 species. As CO_2 uptake is a diffusion process driven by ΔCO_2 , C_4 species will have a higher CO_2 uptake rate than C_3 species at the same atmospheric CO_2 level, because ΔCO_2 is greater. As a result of this CO_2 concentrating mechanism, photosynthesis by C_4 species is independent of O_2 concentration over the range of 2 to 21% (Leopold and Kriedemann 1975).

C_3 and C_4 species exhibit large differences within a group and between groups in their photosynthetic response to temperature (Pearcy and Ehleringer 1984) and in their growth rates (Monteith 1978). Similar differences exist both within C_3 species and between C_3 and C_4 species adapted to growing in different parts of the season. In C_3 species photosynthesis is often almost independent of temperature. The response depends on the photosynthetic photon flux density (PPFD) and CO_2 concentration to which the plants are exposed (Milthorpe and Moorby 1979). The lack of temperature response in C_3 species occurs because the ratio of oxygenase to carboxylase function of RuBP-C:O increases with temperature. C_4 species, because they either lack the PCOC or because it isn't expressed, exhibit a large increase in photosynthesis over the temperature range of 20 to 40 C (Pearcy and Ehleringer 1984). Thus the C_4 pathway can potentially exhibit high photosynthetic rates and this has often been interpreted to be an adaptation to high temperatures (Black 1971). However other factors such as

thermostability of the electron transport system (Pearcy et al. 1977) and the ability to regulate leaf temperature within the optimum range while maximizing photosynthesis may be more important (Leopold and Kriedemann 1975 ; Berry and Bjorkman 1980 ; Gates 1980). These characters are obviously not directly associated with the type of PCRC. C₄ species are native to such diverse habitats as coastal swamps, deserts and tropical forests and these species have widely divergent temperature optima for CO₂ fixation (Ludlow 1976 ; Pearcy and Ehleringer 1984).

Transpiration, water use efficiency, and stomatal regulation

Both water loss and CO₂ uptake by a plant are regulated by stomata which are influenced by both plant and environmental factors. Stomata function primarily to regulate the intercellular CO₂ concentration (c_i) while minimizing water loss, and as the PCRC in C₃ and C₄ species operate at different c_i (Nobel 1983), stomata in these two types behave differently (Farquhar and Sharkey 1982). In C₄ species stomata adjust the leaf conductance to water vapor (g) (which is related to stomatal aperture) relative to CO₂ uptake so that c_i is maintained at 100 to 150 cm³ m⁻³ (Pearcy and Ehleringer 1984). Photosynthesis in C₄ species becomes CO₂ saturated at these levels so that any increase in g would result in a higher transpiration rate (assuming that the atmospheric water potential (ψ_a) and leaf water potential (ψ_l) remain constant) but no increase in CO₂ uptake (Farquhar and Sharkey 1982). In C₃ species, because of the PCOC, photosynthesis does not become CO₂ saturated until c_i is 220 to 260 cm³ m⁻³, at atmospheric O₂ levels. In order to reach

this higher c_i , a greater g is required, as ΔCO_2 is less. At a given photosynthetic rate, g is higher in C_3 than in C_4 species and subsequently water loss or transpiration is greater at equal ψ_a and ψ_l (Farquhar and Sharkey 1982). Therefore C_4 species have a higher potential water use efficiency (WUE=assimilation/transpiration) than C_3 species. At a given g , stomata have a greater effect on water loss than on CO_2 uptake (Farquhar and Sharkey 1982) as the diffusivity of water vapor in air is about 1.56 times that of CO_2 (Nobel 1983). The difference arises from the fact that the speed of diffusion is inversely proportional to the square root of the molecular weight of the gas (Nobel 1983). As a result of these differences in c_i and g the potential WUE of C_4 species is always higher than C_3 species. WUE also depends on ψ_a , so that a C_3 species active during the cool, humid part of the season (wheat) may have a higher WUE than a C_4 species active during hot, dry weather (foxtail). In addition high WUE does not relate to greater tolerance of low ψ_l or low soil water potential (ψ_s). The ability to tolerate atmospheric drought and low ψ_s depends on factors such as osmotic adjustment and leaf morphology which are not obviously correlated with the type of PCRC (Bjorkman 1975 ; Pearcy and Ehleringer 1984).

Nitrogen use efficiency

In both C_3 and C_4 species the photosynthetic capacity is closely correlated with leaf nitrogen (N) content (Pearcy and Ehleringer 1984). RuBP-C:O is the major enzyme in leaves of C_3 species and can account for up to 50% of the total protein levels (Brown 1978). In C_4 species RuBP-

C:O is present in lower amounts and PEP carboxylase is in low amounts relative to RuBP-C:O. Thus for a given unit of CO₂ fixation, C₄ species have much lower N levels and a higher nitrogen use efficiency (NUE=moles CO₂ fixed per mol N present). This efficient use of nitrogen is due to the compartmentation of enzymes in the bundle sheath and mesophyll cells (Black 1985). Nitrate assimilation in the leaf is restricted to these two cell types. In C₄ species NO₃⁻ and NO₂⁻ reduction to NH₃ only occurs in leaf mesophyll cells, i.e there is no reductase activity in the bundle sheath cells, but both cell types can assimilate NH₃ (Black 1985). This selective compartmentation of key enzymes is proposed to be responsible for the high NUE (Black 1985). Brown (1978) suggested that in areas where soil nitrogen is low, C₄ species would have an advantage but there is no evidence to date that C₄ species are preferentially distributed in low soil nitrogen areas (Pearcy and Ehleringer 1984) or that a higher NUE is of ecological advantage (Christie and Detling 1982). However valid comparisons of the NUE of C₃ and C₄ species are difficult to conduct unless ecologically similar species are compared under the same environmental conditions (Nobel 1983).

Quantum yield

C₃ and C₄ species differ not only in their pathway of CO₂ fixation but also in the energy cost or quantum yield (Φ) associated with this CO₂ fixation. The quantum yield is defined as the moles of CO₂ fixed per mole of photons absorbed (Nobel 1983). It is important to consider Φ as a function of photons absorbed rather than incident radiation because pigments in leaves absorb radiation of different wavelengths and

because the energy content of photons varies with wavelength (Milthorpe and Moorby 1979). C_3 species require three ATP and two $NADPH_2$ per mole of CO_2 fixed and for RuBP-C:O regeneration. The PCRC in C_4 species requires two additional ATP to regenerate PEP, so energy costs in terms of ATP are higher than in C_3 species (Salisbury and Ross 1978). In C_3 species Φ is dependent on CO_2 and O_2 concentration, and temperature (Ehleringer and Bjorkman 1977 ; Monson *et al.* 1982). In C_3 species PCO increases relative to PCR, so Φ decreases, but there is no significant temperature effect in C_4 species (Pearcy and Ehleringer 1984). The decrease can be from 0.069 at 14 C to 0.042 at 38 C (Ehleringer and Bjorkman 1977). However there is wide variation in Φ among C_4 species and this may be associated with the subtype pathway (Ehleringer and Pearcy 1983). NADP-ME types, such as green foxtail, have the highest Φ among the C_4 species. The lower Φ in C_4 species results in greater energy costs and is the only known disadvantage of the C_4 PCRC (Ehleringer 1978), but this disadvantage only occurs at temperatures less than 18 to 23 C (Ehleringer and Pearcy 1983). Within this leaf temperature range Φ is greater for C_3 than for C_4 species. For single leaves the C_4 pathway is possibly most advantageous under high PPF, high temperature and limited water supply but at the canopy level the lower Φ can be a disadvantage due to shading (Ehleringer 1978).

Geographic distribution and ecological diversity

Geographical studies have shown that there is generally a greater abundance of C_4 species in warmer environments, but the distinction must