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A Comparison of the Growth of the C_4 Grass *Spartina anglica* with the C_3 Grass *Lolium perenne* at Different Temperatures

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ABSTRACT

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S. anglica is one of the few C_4 species which occurs naturally in cool temperate zones. It is known to attain photosynthetic rates which equal or exceed those of C_3 grasses over the temperature range typical of the spring and summer in cool temperate climates. This study examines whether *S. anglica* can also attain comparable growth rates at these temperatures. Seedlings of *S. anglica* and *L. perenne* cv. S23 were grown in controlled environments at 10, 15, 20 and 25 °C. Quantitative growth analysis was conducted by taking frequent harvests to determine the progressions of leaf area and plant weight of individual plants with time. Quadratic regressions were found to describe these progressions well. Instantaneous derived growth parameters were calculated from the fitted regressions. Both absolute and relative growth rates of *S. anglica* were significantly lower than for *L. perenne*, this being largely attributable to a lower ratio of leaf area production per unit of plant dry weight. Although the amount of dry matter invested into leaves was similar, the leaf area per unit of leaf dry weight was lower in *S. anglica*. In comparison to *L. perenne*, the rate of dry matter accumulation per unit of leaf area (*ULR*) was higher in *S. anglica* at 25 °C and initially equal at 10 °C. Prolonged exposure to 10 °C steadily reduced *ULR* in *S. anglica* which approached zero at 80 d. Although growth in *S. anglica* is reduced more by low temperature than it is in *L. perenne*, by comparison to other C_4 species the assimilatory capacity of *S. anglica* is more tolerant of low temperature exposure.

Key words—C_4 photosynthesis, temperature, quantitative growth analysis.

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INTRODUCTION

Spartina anglica Hubb. is an amphidiploid derived from the infertile *Spartina* × *townsendii* H. & J. Groves which resulted from the putative hybridization of *Spartina alterniflora* Lois. and *Spartina maritima* (Curt.) Fernald in Southampton Water (Goodman, Braybrook, Marchant, and Lambert, 1968; Hubbard, 1984). In roughly 100 years *S. anglica* and smaller quantities of *S.* × *townsendii* have spread by natural dispersal and planting to occupy more than 24 000 ha of coastal salt marsh in N.W. Europe (Ranwell, 1967; Long and Mason, 1983). Of the known C_4 species of N.W. Europe only *S. anglica* and *S. townsendii* form major components of the

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communities in which they occur (Long, 1983). Other native C_4 species, which include *Cyperus longus* L., *Atriplex laciniata* L., *Salsola kali* L. and *Spartina maritima*, are only rare or occasional species within their native communities (Long, Incoll, and Woolhouse, 1975; Jones, Hannon, and Coffey, 1981; Long, 1983). The apparent success of *S. anglica* in cool temperate regions is unique for a plant which shows the features typical of C_4 species, i.e. the first products of photosynthetic CO_2 assimilation are C_4 compounds (Thomas and Long, 1978; Smith, Woolhouse, and Jones, 1982), it has Kranz leaf anatomy, a low photosynthetic CO_2 compensation point (Long *et al.*, 1975) and a low photorespiratory rate (Long and Woolhouse, 1978*a*). In general, the maximum rates of CO_2 assimilation by individual leaves of C_4 grasses are much greater than those of C_3 grasses. These maxima in C_4 grasses are usually achieved at temperatures of 35–40 °C. At 15 °C and below, the rate of CO_2 assimilation in C_4 grasses is inferior to rates reported for C_3 grasses. *S. anglica* is an exception to this generalization with rates of CO_2 assimilation by single leaves approximately equal to those of temperate C_3 grasses at leaf temperatures of 5 °C and 10 °C and are significantly greater at 15 °C and above (Long and Woolhouse, 1978*b*).

Maximum short-term growth rates and annual dry-matter yields of C_4 species exceed those of C_3 species (Beadle, Long, Imbamba, Hall, and Olembo, 1985), but these higher maxima are only realized at high temperatures and growth rates decrease markedly with decrease in temperature, becoming inferior to those of C_3 grasses in cool conditions (Tainton, 1967). Since *S. anglica* shows adaptation of its CO_2 assimilatory apparatus to lower temperatures and has rapidly colonized inter-tidal mud-flats at a number of sites in N.W. Europe, it could be suggested that this C_4 species is an exception capable of growth rates comparable to C_3 grasses at low temperatures. This suggestion is examined by comparing the growth of *S. anglica* with a temperate C_3 grass at different temperatures. Growth responses to temperature, at the level of individual plants, are the result of the combined responses of net assimilation, assimilate distribution and morphogenesis. To obtain basic information on each of these responses a quantitative plant growth analysis was conducted. Although there have been many previous quantitative growth analyses of C_3 grasses in controlled environments, few have examined growth at more than two temperatures. Therefore, a direct comparison was made by growing a C_3 grass alongside *S. anglica* in four temperature regimes. *Lolium perenne* L. (cv. S23) was chosen for this comparison because, like *S. anglica*, it is a long-lived perennial, but it has also been specifically selected for high productivity.

MATERIALS AND METHODS

Plant material and growth conditions

Seeds of *S. anglica* were collected at Southport, Lancs., in mid-November and stored for 2 weeks over seawater at 4 °C. This procedure improved subsequent germination and seedling survival. Seed of both species was germinated at 20 °C and the seedlings planted individually in 13 cm diameter pots of compost (EFF Ltd.). Seedlings were graded by height into six groups from which equal numbers were allocated at random to four controlled environment rooms (Ford and Thorne, 1975), initially at 20 °C. Seedlings were acclimatized over a 2 week period by a gradual change in temperature to the final growth conditions. The growth analysis commenced at the end of this acclimatization period. The air temperatures in the four rooms were 25, 20, 15 and 10 °C with the lights on and 3 °C lower in each room with the lights off. For brevity, treatments will subsequently be referred to only by their 'day-time' temperatures. The lights in each room supplied a mean photon flux density of 510 μmol m^{-2} s^{-1} at pot height during the 14 h photoperiod and the water vapour pressure deficit was maintained at 0·5 kPa.

Sampling procedure

For all combinations of species and temperature, twelve harvests of six plants each were made; the intervals between harvests varied according to the growth rate. Harvests were at 3–4 d intervals for plants of both species at 25 °C and 20 °C, and for *L. perenne* at 15 °C but at 7 d intervals for both species

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at 10 °C and for *S. anglica* at 15 °C. The plants of each species were divided into six groups according to height. At each harvest one plant was randomly selected from each of the six height groups in each treatment (Ford and Thorne, 1975).

The harvested plants were washed and divided into: (1) roots and rhizomes; (2) stems, leaf sheaths and enclosed lamina; (3) emerged lamina. The projected lamina area was determined using an electronic planimeter (Paton Industries Ltd.) and then all fractions were dried to constant weight in a forced-draught oven at 90 °C.

Growth analysis

To avoid the limitations of classical growth analytical procedures, frequent harvests of small samples were made and polynomial regression lines fitted to the progression of weight and leaf area with time (Radford, 1967; Hunt and Parsons, 1974). This procedure allows the calculation of growth parameters and their statistical confidence limits at any instant in time (Hunt, 1983). Second order polynomials (quadratic) gave a significantly improved fit over first order polynomials (linear) to the progression of the natural logarithms of weight and area against time in all cases. No further improvement of fit was achieved to the data as a whole by use of third order (cubic) polynomials, as determined by the procedure of Hunt and Parsons (1974).

Quadratic regressions were fitted to the progression of the natural logarithms of dry weight and leaf area by the least squares procedure of Nicholls and Calder (1973). Computations were made on a DEC-10 computer system (Digital Corp.) using a FORTRAN-10 program modified from a listing provided by Dr A. G. Nicholls, C.S.I.R.O. Instantaneous derived growth quantities were calculated from curves fitted to the measured quantities. To simplify species and treatment comparisons, the data are presented in the form of temperature response curves. Low temperature retards development, thus to avoid comparison of plants at different stages of development, curves were constructed using derived growth quantities calculated at a dry weight common to both species for all temperature treatments. A similar approach was used by Paul, Hardwick, and Parker (1984) to minimize ontogenetic drift in an analysis of temperature effects on tomato growth.

RESULTS

Dry weight and leaf area

Quadratic regression lines provide a close fit to measured weights and leaf areas at all temperatures without any obvious systematic deviations of fitted values from those observed (Fig. 1). The rate of increase in dry weight (W) and leaf area (L_A) of *L. perenne* was, by comparison to *S. anglica*, greater at all temperatures and less sensitive to decrease in temperature (Fig. 1). For example, after 38 d the leaf area (L_A) of *L. perenne* at 10 °C was approximately 16% of that at 25 °C, whilst in *S. anglica* the L_A at 10 °C was only 4·5% of that at 25 °C (Table 1).

Relative growth rate

Both relative dry matter (RGR) and relative leaf area ($RLGR$) growth rates declined as the seedlings became older. This is indicated by the progressions of the natural logarithms of weight and leaf area against time (Fig. 1). After 38 d in the respective experimental temperatures, the mean dry weight (W) of *S. anglica* was lower than that of *L. perenne* (Table 1), and as the dry weights of both species did not differ significantly at the start of the experiment, it follows that RGR was lower in *S. anglica* (Fig. 2a), i.e. the efficiency of dry weight accumulation per unit of existing dry weight was lower in *S. anglica* throughout the growth period. The RGR of both species was significantly reduced by decreasing temperature, the reductions being proportionally greater in *S. anglica* (Fig. 2a). The lower RGR of *S. anglica* could result from a lower unit leaf rate (ULR) and/or a lower leaf area ratio (LAR).

In both species relative leaf growth rate ($RLGR$) was significantly decreased by lower temperatures (Fig. 2b). $RLGR$ was significantly lower in *S. anglica* than in *L. perenne* at all

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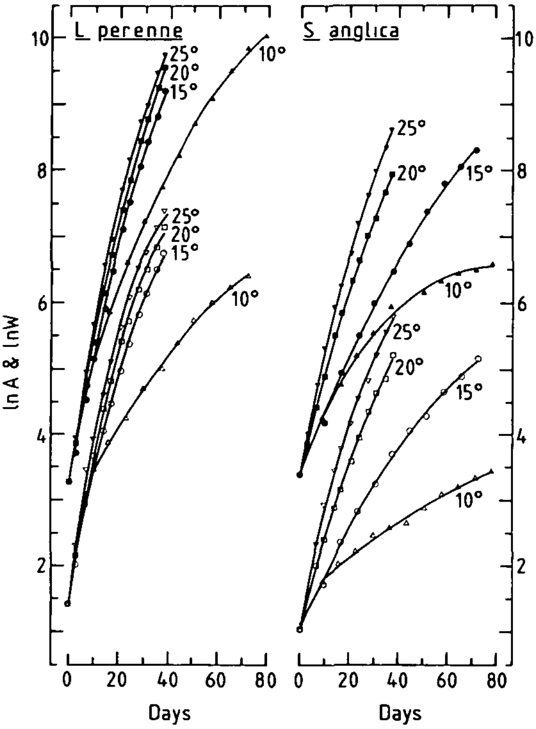

FIG. 1. Fitted quadratic regressions of the natural logarithms of dry weight (ln W, closed symbols) and leaf area (ln A, open symbols) with time. The plotted symbols are the actual mean values of the experimental data for *L. perenne* (a) and *S. anglica* (b) grown at four different day/night air temperatures (▲△ 10/7 °C; ●○ 15/10 °C; ■□ 20/15 °C; ▼▽ 25/20 °C); only day temperatures are indicated on the figure.

TABLE 1. *Comparison of the mean dry weights and leaf areas, per plant ± their standard errors, after 38 d*

Species	Temperature (°C)	Plant dry weight (W)	Plant leaf area (L_A)
S. anglica	25	5·87±0·40	351±23
	20	3·03±0·36	188±18
	15	0·82±0·25	42± 6
	10	0·47±0·06	16± 2
L. perenne	25	17·43±1·07	1643±66
	20	14·93±0·99	1283±67
	15	9·98±0·54	863±59
	10	4·92±0·54	260±28

temperatures, and this difference increased with decrease in temperature (Fig. 2b). The *RLGR* for *S. anglica* was 30% lower than for *L. perenne* at 25 °C, but 73% lower at 10 °C.

Unit leaf rate and leaf area ratio

The rates of dry matter accumulation per unit of leaf area, the so-called unit leaf rates (*ULR*), of plants of *S. anglica* were strongly dependent on temperature, whilst the *ULR* of *L.*

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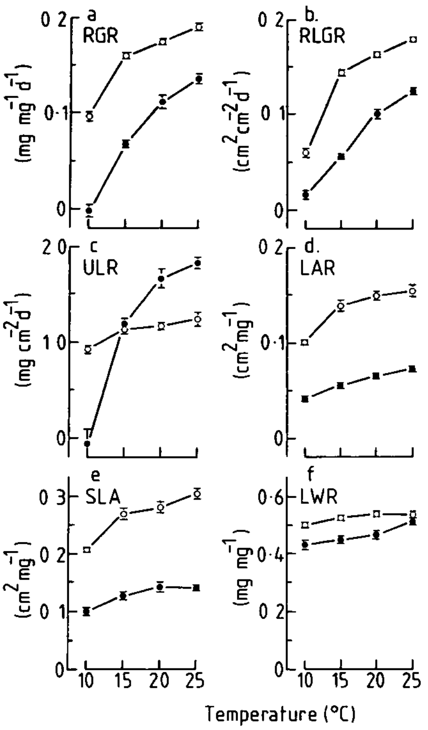

FIG. 2. (a) Relative growth rate (mg mg^{-1} d^{-1}), (b) relative leaf growth rates (cm^2 mg^{-1} d^{-1}), (c) unit leaf rate (mg cm^{-2} d^{-1}), (d) leaf area ratio (cm^2 mg^{-1}), (e) specific leaf area (cm^2 mg^{-1}) and (f) leaf weight ratio (mg mg^{-1}) ± one standard error for *S. anglica* (●) and *L. perenne* (○) against temperature (°C). All points are the fitted instantaneous values when plants had reached a dry weight of 710 mg.

perenne showed no significant variation with temperature except for a decrease at 10 °C (Fig. 2c). By comparison to *L. perenne*, *S. anglica* showed a *ULR* which was higher at both 20 °C and 25 °C, similar at 15 °C and lower at 10 °C (Fig. 2c). However, there were marked changes in *ULR* with time at 10 °C. Initially the *ULR* of *S. anglica* at 10 °C was slightly higher than that of *L. perenne*, but it declined with time and was almost zero at 80 d (Fig. 3). The consistently lower *RGR* of *S. anglica* at all temperatures cannot then be attributed to a lower

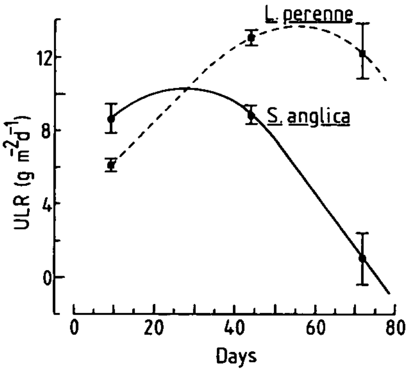

FIG. 3. The effect of prolonged exposure to 10 °C (70 d) on the fitted unit leaf rates (mg cm^{-2} d^{-1}) ± their standard errors, for *S. anglica* (●) and *L. perenne* (■).

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ULR, except after prolonged exposure to 10 °C. The lower *RGR* values must, therefore, result from a lower leaf area ratio (*LAR*), i.e. the amount of leaf area per unit of plant dry weight.

The *LAR* of *S. anglica* declined steadily with temperature, such that its value at 10 °C was *c.* 55% of *LAR* at 25 °C (Fig. 2d). In *L. perenne*, *LAR* was only significantly lower at 10 °C. At all temperatures, the *LAR* of *S. anglica* was only 40-50% of that of *L. perenne* (Fig. 2d). This major difference could be due either to a lower proportion of dry weight invested in leaves (leaf weight ratio; *LWR*), a higher leaf weight per unit of leaf area (specific leaf area; *SLA*), or a combination of the two.

Specific leaf area and leaf weight ratio

The lower *LAR* values observed for *S. anglica* were clearly the result of a lower *SLA*, since the leaf weight ratios (*LWR*) of *S. anglica* were only slightly lower than those of *L. perenne* (Fig. 2b, e, f). Thus the lower *RGR* of *S. anglica* (Fig. 2a), was largely the result of a lower *SLA*. A significant decline in *SLA* of about 30%, from 25 °C to 10 °C in both species (Fig. 2e) implied that the leaves became thicker at the lower temperatures. No significant decrease in *LWR* with decreased temperature occurred in *L. perenne*, but there was a significant decrease in *LWR* of *S. anglica* at the lower temperature (Fig. 2f), reflecting an altered distribution of dry weight within the plant. The distribution of dry weight between organs is illustrated in Fig. 4. At lower temperatures, the below-ground organs of *S. anglica* contained a greater, and the leaves a lesser, proportion of total dry weight compared to plants grown at higher temperatures (Fig. 4a). A similar, but less marked trend is seen in *L. perenne* (Fig. 4b).

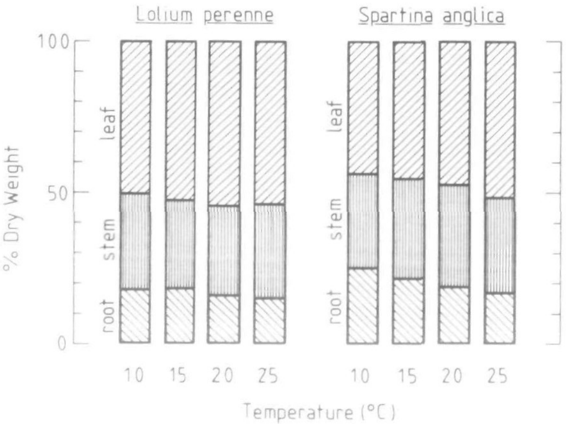

FIG. 4 The distribution of dry weight in (a) *S. anglica* and (b) *L. perenne* when plant had grown to a dry weight of 710 mg expressed as a percentage of the total dry weight in (LEAF) emerged leaf lamina; (STEM) stems, sheaths and enclosed young lamina; and (ROOT) roots and rhizomes.

DISCUSSION

Absolute and relative growth rates both in terms of dry weight (Figs 1a, 2a) and leaf area (Figs 1b, 2b) were clearly higher in *L. perenne* by comparison to *S. anglica*. The cause of the differences in *RGR* may be analyzed since the instantaneous *RGR* is the exact product of the instantaneous unit leaf rate (*ULR*) and leaf area ratio (*LAR*).

From previous photosynthetic studies (Long and Woolhouse, 1978*b*), and assuming no major differences in respiratory losses between the two species and negligible self-shading, *ULR* in *S. anglica* would be expected to be greater or equal to *ULR* in *L. perenne*. The *ULR* of

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S. anglica was in fact greater at 25 °C, but was markedly lower at 10 °C, for plants of the same dry weight (Fig. 2c). The previous photosynthetic studies were made on plants grown at 16 °C (Long and Woolhouse, 1978*b*). In the present study, the *ULR* in *S. anglica* was not significantly different from the *ULR* in *L. perenne* for the first 25 d at 10 °C (Fig. 3); beyond this time *ULR* declined rapidly in *S. anglica* but not in *L. perenne*. Self-shading would seem the likely cause of the indicated decrease in the *ULR* of *L. perenne* at 10 °C after 60 d (Fig. 3) since the leaf area index exceeded 3 at this stage. Self-shading would not explain the far more pronounced decrease of *ULR* in *S. anglica* at 10 °C (Fig. 3) since its leaf area index was less than 0·2 at 60 d. Thus, either the assimilatory capacity in *S. anglica* is reduced or respiration increased by prolonged exposure to 10 °C. Field measurements of photosynthesis in *S. anglica* have similarly suggested an inhibitory effect of low temperature pre-history on assimilatory capacity. Leaves growing in the field during winter and spring showed lower net rates of CO_2 uptake when compared, at any one temperature, with leaves growing in the summer (Long and Incoll, 1979; Dunn, Long, and Thomas, 1981; Dunn, 1981). The slow decline in assimilatory capacity over many days at 10 °C, indicated by *ULR* in *S. anglica*, contrasts markedly with observations of other C_4 species. Exposure to 5 °C or 10 °C, even for a few hours, results in permanent damage to the assimilatory capacity of *Z. mays* leaves (Long, East, and Baker, 1983). Plants of *Sorghum bicolor* grown at 10 °C for 2 d showed pronounced necrotic lesions (Taylor and Rowley, 1971), which followed chloroplast ultrastructural damage (Taylor and Craig, 1971). No such lesions were observed on any *S. anglica* plant throughout the entire experiment. Whilst *S. anglica* at a field site in S.E. England retained some green and apparently healthy leaves throughout the year (Dunn, 1981).

Although *ULR* was higher in *S. anglica* than in *L. perenne* at 20 °C and above, and initially equal at 15 °C and 10 °C, *RGR* was always lower in *S. anglica* (Figs 2, 3). This was due to the lower leaf area ratio (*LAR*) of *S. anglica*, which was on average less than half that of *L. perenne* at all growth temperatures. *LAR* is the product of specific leaf area (*SLA*) and leaf weight ratio (*LWR*). *SLA* in both species was depressed by growth at 10 °C compared to 25 °C, the depression being greater for *L. perenne*. Temperature induced decrease in *SLA* of C_3 species has been reported previously (Mitchell, 1953; Beevers and Cooper, 1964; Robson and Jewiss, 1968; Woodward, 1979; Paul *et al.*, 1984). The accumulation of assimilate associated with the decreasing *SLA* at low temperatures may result from decreased use of assimilate in leaf growth, and the accumulation of untranslocated photo-assimilate (Robson and Jewiss, 1968; Hilliard and West, 1970). Decreased *SLA* induced by low temperature has also been associated with decreased cell division and extension (Beevers and Cooper, 1964; Kleinendorst and Brouwer, 1972; Woodward, 1979), which results in shorter and thicker leaves (Cooper, 1964; Ryle, 1964). Forde, Whitehead, and Rowley (1975) concluded that the processes utilizing photo-assimilate, such as respiration, translocation, cell division and enlargement, were decreased more by low temperature than was photosynthesis in the C_4 grass *Paspalum dilatum*. Duncan and Hesketh (1968) showed that photosynthetic rates of individual leaves of a number of *Zea mays* cultivars were less sensitive to decrease in temperature than the relative leaf growth rate (*RLGR*). Jones *et al.* (1981) similarly showed that leaf extension growth in the temperate C_4 species *Cyperus longus* was decreased more by reduction in temperature to 10 °C than was photosynthetic rate. Thus, a decreased *SLA* due to accumulation of assimilate in the leaf could be expected. Although the *SLA* of *L. perenne* at 10 °C was significantly lower than at 25 °C, the *LWR* was not (Fig. 2f). This indicates that the leafiness of *L. perenne* was only depressed on an area but not on a weight basis. In *S. anglica* both the *SLA* and the *LWR* at 10 °C were significantly lower than at 25 °C (Fig. 2e, f), showing that the leafiness of *S. anglica* was significantly reduced at 10 °C compared to 25 °C

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on both a leaf area and a leaf weight basis. The diversion of a greater proportion of dry weight to the below-ground organs (Fig. 4) as well as the production of thicker leaves would have reduced the assimilate available for leaf growth, and thus would reduce the growth of *S. anglica* at 10 °C.

These results suggest that for *S. anglica* in the field *ULR* would be very low until mean temperatures rose above 10 °C. This agrees closely with previous studies of *S. anglica* photosynthesis in the field which show that the capacity of leaves for CO_2 uptake is low until mean temperatures have exceeded 10 °C in early summer (Long and Incoll, 1979). Similarly, significant production of new dry matter by *S. anglica* on a salt marsh in E. England did not begin until June or July, two months later than in a C_3 grass, *Puccinellia maritima* growing on a nearby saltmarsh (Dunn *et al.*, 1979).

In conclusion, the growth of *S. anglica* is by comparison to *L. perenne* strongly limited by low temperature in two important respects. First, the rate of leaf area development is close to zero at 10 °C. Secondly, whilst the rate of dry matter assimilation per unit of leaf area (*ULR*) at 20 °C and above is higher, prolonged exposure to 10 °C results in a slow decline in *ULR* to zero. The major difference between *S. anglica* and other C_4 grasses appears to be that exposure of leaves to 10 °C resulted in only a slow decline in *ULR* over 80 d compared to a sudden loss of assimilatory capacity or even leaf death within two to three days of similar exposure of *Zea mays* and *Sorghum bicolor* (Taylor and Rowley, 1971; Long, 1983; Long *et al.*, 1983).

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