Effects of water stress on the leaf demography of *Agropyron desertorum*, *Agropyron dasystachyum*, *Bromus inermis*, and *Stipa viridula*

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We examined the effect of water stress on leaf demography in four grass species known to differ in degree of drought resistance. Stress was imposed by growing plants in solution culture and lowering water potential of the solution either slowly, or rapidly, by the addition of polyethylene glycol. Rapid stress reduced the number of leaves by increasing leaf death rate and decreasing birth rate. Gradual stress reduced the number of leaves by temporarily decreasing leaf birth rate; death rate also decreased, partially compensating for the reduction in birth rate. Death rates were age specific; rapid stress had little effect on young leaves, and gradual stress increased leaf longevity to the greatest extent in those leaves that emerged immediately prior to the imposition of stress. As a result, plants subjected to rapid stress had a young leaf age structure, while plants subjected to gradual stress had an older age structure. Differences among species in tolerance to water stress were related in part to differences in leaf age structure. Species with a young leaf age structure exhibited less of an increase in leaf mortality in response to rapid stress, and more of an increase in leaf longevity in response to gradual stress than other species.

Key words: drought tolerance, leaf turnover, leaf age structure, polyethylene glycol, leaf senescence.

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Les auteurs ont examiné les effets du stress hydrique sur la démographie foliaire chez quatre espèces herbacées connues pour leurs capacités différentes à résister à la sécheresse. Le stress a été appliqué en cultivant les plantes en solution de culture et en abaissant le potentiel hydrique de la solution, lentement ou rapidement, en ajoutant du polyéthylène glycol. Le stress rapide réduit le nombre de feuilles en augmentant le taux de mortalité des feuilles et en diminuant le développement de nouvelles feuilles. Le stress progressif réduit le nombre de feuilles en diminuant temporairement le développement de nouvelles feuilles; le taux de mortalité des feuilles diminue également, compensant partiellement pour la réduction de l'apparition de nouvelles feuilles. Les taux de mortalité sont liés à l'âge; le stress rapide affecte peu les jeunes feuilles, et le stress progressif augmente le plus fortement la longévité des feuilles qui se sont formées immédiatement avant l'application du stress. Il s'ensuit que les plantes soumises au stress rapide montrent une structure d'âge plus jeune, alors que les plantes soumises au stress progressif ont une structure d'âge plus vieille. On peut relier les différences entre les espèces, quant à leur tolérance à la sécheresse, en partie avec les différences dans les structures d'âge. Les espèces ayant une structure d'âge jeune montrent une plus faible augmentation de la mortalité foliaire sous l'influence du stress rapide, et plutôt une augmentation de la longévité des feuilles sous l'influence d'un stress progressif, que les autres espèces.

Mots clés : tolérance à la sécheresse, dynamique foliaire, structure d'âge foliaire, polyéthylène glycol, sénescence foliaire.

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Introduction

Much of the variation in plant size in response to the environment can be explained by changes in numbers of repeatable units (e.g., individual leaves and roots). Harper and White (1974) argued that the application of demographic techniques to the populations of modules that make up individual plants can provide useful insights to the response of plants to environmental changes. Bazzaz and Harper (1977) applied formal demographic analysis to leaf numbers in *Linum* and used this information to interpret its response to light, density, and soil nutrient availability. They point out that both birth rates (i.e., photosynthetic contribution to new leaves) and death rates are age specific. Therefore, to understand how plant growth responds to the environment, it is necessary to know both the age structure of the leaf population, and the response of individual cohorts that make up this population.

Studies of marked leaves in the field indicate that the dynamic nature of grass leaf populations is related in general to environmental conditions (Maxwell 1977; Williamson 1976;

Vine 1983; Gounot and Yu 1980). The effects of water stress on leaf growth and senescence in grasses have been studied extensively (e.g., Hunt 1970; Kleinendorst 1975; Majerus 1975; Chu and McPherson 1977; Ludlow and Ng 1976, 1977; Chu et al. 1979; Horst and Nelson 1979), but not by using demographic analysis. These studies reveal the effect of water stress on leaf birth and death, but do not examine the effect of population age structure upon response, nor how water stress may affect this structure.

Our study examines how water stress influences leaf demography in four grass species under controlled environment conditions: *Bromus inermis* Leyss., *Agropyron desertorum* (Fisch.) Shutt., *Stipa viridula* Trin., and *Agropyron dasystachyum* (Hook.) Scribn. These species are all adapted to the Northern Great Plains region of North America but differ in origin and the extent to which they tolerate water stress (Looman 1983; Redmann 1985; Knowles 1987). *Agropyron desertorum* and *A. dasystachyum* are adapted to drier sites than *B. inermis* and *S. viridula*. *Bromus inermis* and *A. desertorum* were introduced to western Canada from Europe and central Asia, respectively, while *A. dasystachyum* and *S. viridula* are native to western Canada. Since the rate at which water stress develops may influence the response of plants, we compared

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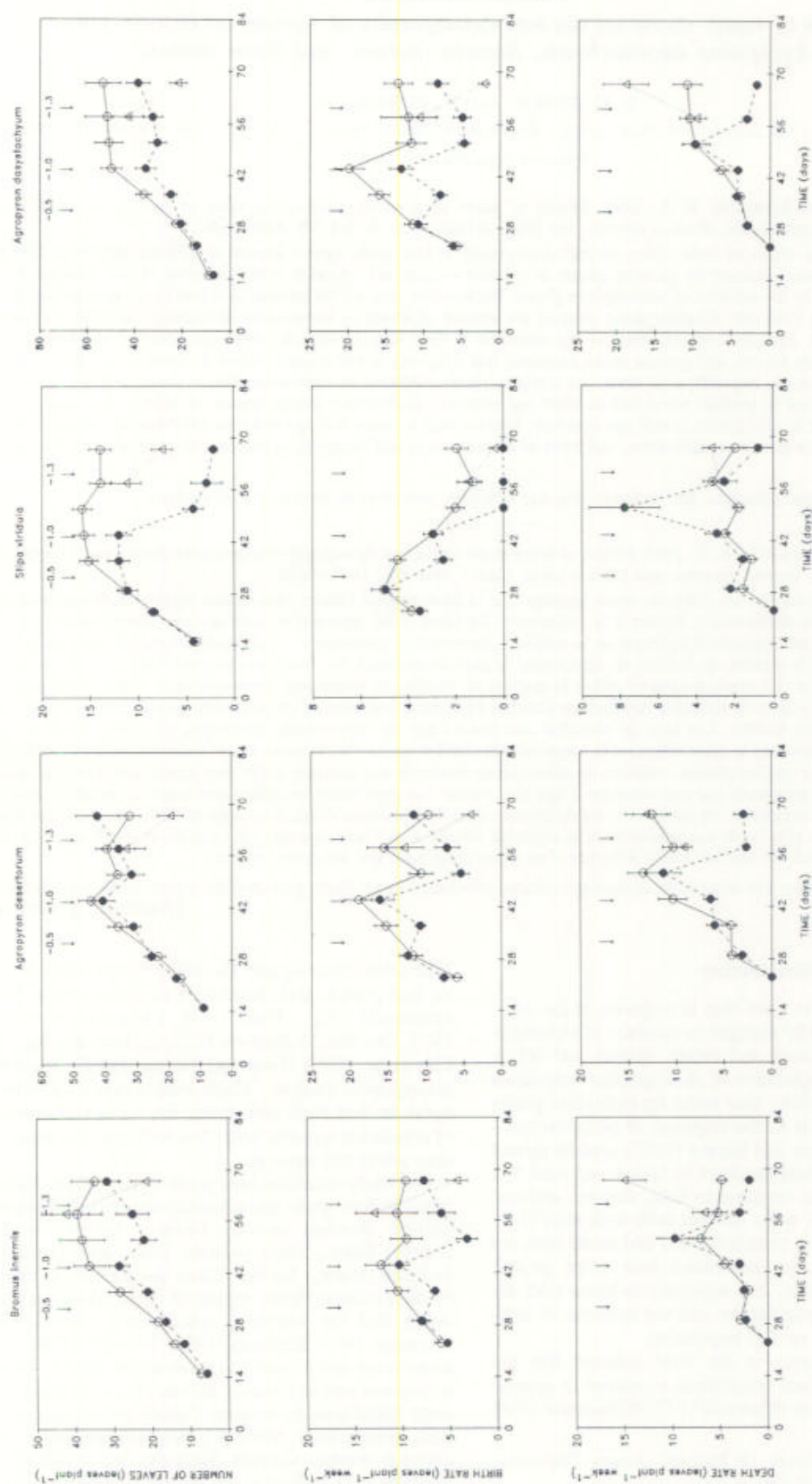
Fig. 1. Leaf number, birth rate, and death rate for plants subjected to either no stress (○), slow stress (●), or rapid stress (△). Proceeding from left to right, the three arrows at the top of the figures indicate (*i*) time at which solution potential of the slowly stressed plants was lowered to −0.5 MPa, (*ii*) time at which solution potential of the slowly stressed plants was lowered to −1.0 MPa, and (*iii*) time at which solution potential of both the slowly stressed and rapidly stessed plants was lowered to −1.3 MPa. Birth and death rates are average values over the census intervals. Error bars are ± 2 SE.

species under rapidly stressed, gradually stressed, and unstressed conditions. Degree and rate of stress were controlled by growing plants in solution culture and adjusting water potential of the solution by the addition of polyethylene glycol. Results provide insights into the strategies that determine a species survival under drought conditions.

Methods

Seeds were germinated in flats filled with moist vermiculite. At the 2- to 3-leaf stage they were transplanted into 10-L plastic trays filled with Evan's modified Shive nutrient solution (Salisbury and Ross 1978). Each seedling, mounted in a split foam rubber plug, was placed into holes cut in a styrofoam sheet resting on top of the plastic trays. Nine plants of each of the four species were randomly positioned in each of six trays (36 plants per tray). The trays were placed within a controlled environment chamber that provided an irradiance of 1200 μmoles m^{-2} s^{-1}, a constant temperature of 20°C, and a 12-h photoperiod. The nutrient solution in each of the six trays was replaced at weekly intervals and was aerated constantly. The sides of the trays were covered with aluminum foil to prevent algal growth. The six trays were periodically rotated among positions within the chamber.

Seedlings were allowed to grow for a period of 5 weeks before the experiment was initiated. At this point (day 0 of the experiment) all living leaves on each of the individual plants were labelled by loosely placing a circle of plastic-covered wire around each leaf. Thereafter, at approximately weekly intervals, all newly emerged leaves were labelled with a different colored plastic wire, and the number of births were recorded. A leaf was considered fully emerged when the collar region of the leaf was visible above the culm (i.e., when the entire leaf blade had emerged). At the same time, the number of deaths in each of the previous cohorts was recorded, and the dead leaves together with their tags were removed. A leaf was not considered dead until the entire leaf blade had turned brown.

From day 0 to day 31 all six trays were treated in the same fashion. Water potential in two of the trays (gradual stress treatment) was lowered to −0.5, −1.0, and −1.3 MPa on days 32, 43, and 60, respectively. Water potential of two more trays was lowered to −1.3 MPa in one step at day 60 (rapid stress treatment). The remaining two trays remained at the water potential of the nutrient solution (> −0.1 MPa) for the entire course of the experiment (unstressed plants). The changes in water potential in the two stress treatments were an attempt to simulate the rate at which water stress might develop on deep, fine-textured soils (gradual stress) and shallow, course-textured soils (rapid stress). Water potential was lowered by the addition of polyethylene glycol. To avoid the problems associated with the uptake of low molecular weight molecules (Kaufmann and Eckard 1971) we used Carbowax® 8000 (mol. wt. 7000–9000, Union Carbide Corporation). Solutions were aerated constantly to avoid oxygen depletion (Michel 1971). Although polyethylene glycol is widely used to impose controlled levels of water stress, the possibility of direct toxicity cannot be eliminated (Plaut and Federman 1985). Nevertheless, we are reasonably confident that the responses described below are a reflection of water stress rather than toxicity, as responses were in accord with the known sensitivity of the species to drought.

Initially, births and deaths were recorded for all plants (i.e., 18 plants per species per treatment). At day 44, owing to the large number of leaves, 10 of the 18 plants were randomly selected to continue the census for the rest of the experiment. There was some variation among species and treatments in the number of plants sampled due to mortality of individual plants. There were 10 plants (out of a total of 216) that did not establish properly and died within the first 2 weeks of the experiment. As the deaths were unrelated to treatment, these plants were dropped from the experiment entirely. Mortality of established plants occurred only in the gradual stress treatment during the last census interval. Census data for these plants (a total of nine individuals) were included in the analysis.

At harvest (day 67), shoots were divided into leaf blades and culms (including leaf sheaths), dried at 40°C until there was no further loss in weight, and then weighed. Roots were not harvested because it was not possible to separate the roots of individual plants. Separate weights were obtained for each leaf age cohort. Biomass data were used to construct a leaf age profile by expressing biomass of each leaf cohort as a proportion of total leaf biomass. Mean age of leaves was determined by weighting each cohort by its biomass and calculating the average weighted age of all leaf cohorts on a given plant. The leaves that had not yet fully emerged at the time of harvest were excluded from this analysis.

Differences among species and treatments in the number of leaves per plant, birth rate per plant, and death rate per plant were examined by calculating the mean and standard error for each treatment–species combination at a given time and plotting the results. As the number of leaves per plant will affect birth and death rates expressed on a per plant basis, births and deaths for the last census interval (days 58–67) were also expressed as a proportion of the number of leaves at the start of the census interval (day 58). Two by two contingency tables were used to examine differences in these proportions among treatments. Cohort specific mortality was examined by plotting survivorship curves for each cohort.

Biomass data were analyzed by split-plot analysis of variance with trays as main plots. The treatment design was factorial, with the three water stress treatments crossed with the four species. The main effect of the water stress treatments was tested using the main plot error term. The main effect of species and the species × water stress interaction were tested using the residual error term. A priori paired t-tests were used to determine the significance of differences among selected treatment means. All proportional data were transformed prior to statistical analysis using the arcsin transformation. In addition to the univariate analyses of variance, multivariate analysis of variance was used to examine overall differences in age structure among species and treatments. Dependent variables were the proportional allocations to each of the leaf cohorts. As the older cohorts were largely dead by the time of harvest, cohorts 1–4 were combined into a single dependent variable for this analysis. In the case of the total leaf biomass data, the species had substantially different means and consequently different variances. For these data, separate analyses were conducted for each of the four species and as there was never a significant main plot error term, this term was combined with the residual error to increase the number of degrees of freedom for testing the effect of treatment. The 0.05 level of probability was used for all tests of significance.

Results

Number of leaves

In all four species, rapidly induced stress resulted in a decline in the number of leaves per plant relative to unstressed controls (Fig. 1, day 67). The two introduced species (*B. inermis* and *A. desertorum*) exhibited less of a decline (38 and 40%, respectively) than the two native species (*S. viridula*, 46% and *A. dasystachyum*, 59%). Leaf birth rates per plant declined in all four species and death rates increased in all species except *A. desertorum*. The decline in birth rate per leaf was more marked in the native species (*S. viridula* and *A. dasystachyum*) than in the introduced species (Table 1).

The effect of gradual stress on the number of leaves varied depending upon species (Fig. 1). The most extreme response was observed in *S. viridula*, where the number of leaves in the gradually stressed plants was reduced to well below that of the rapidly stressed plants. In *A. desertorum* on the other hand, the number of leaves in gradually stressed plants did not decline relative to unstressed plants. *Bromus inermis* and *A. dasystachyum* were intermediate between these two species in their response.
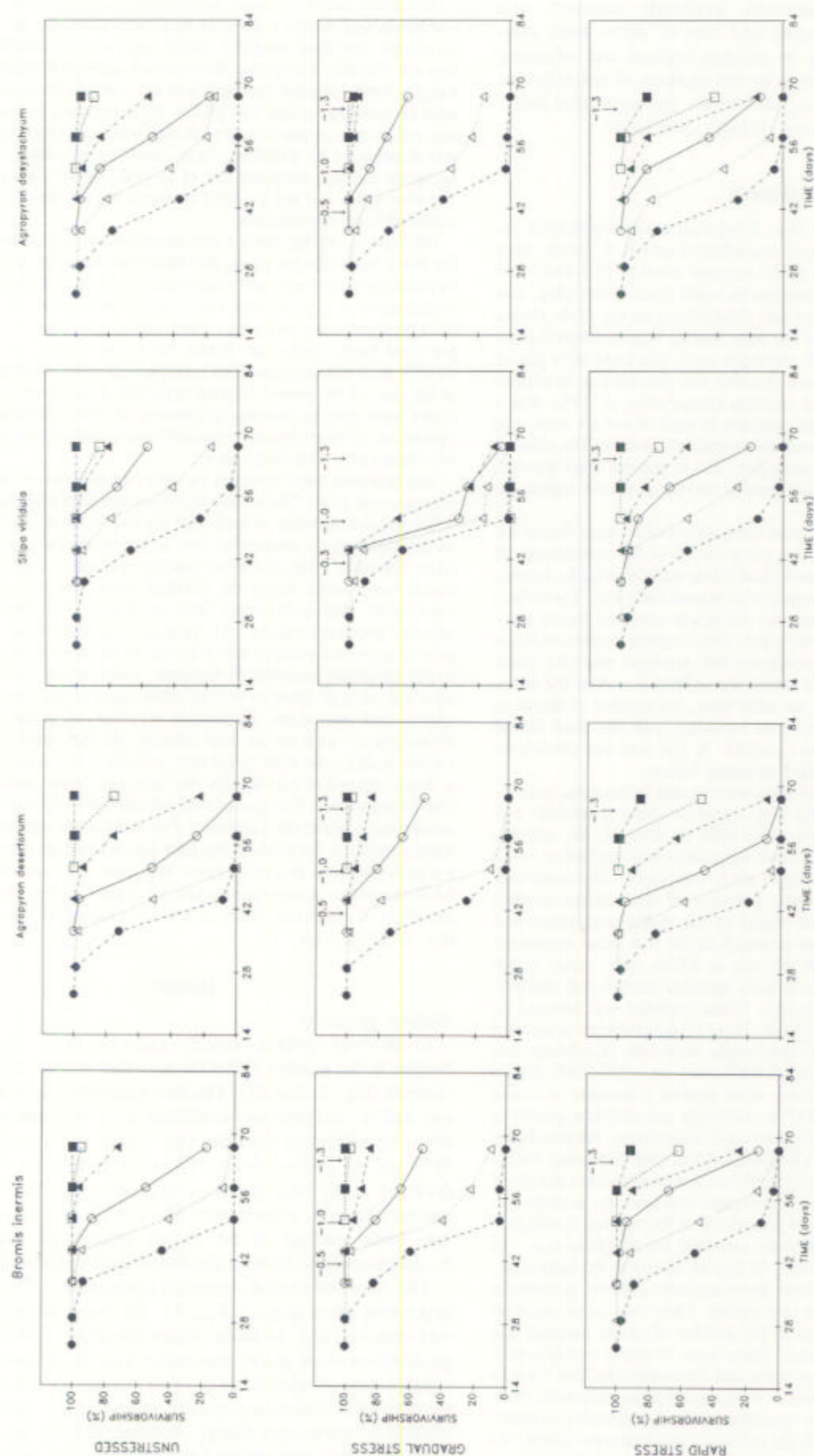
Fig. 2. Cohort specific survivorship of plants subjected to either no stress, gradual stress, or rapid stress. Proceeding from left to right, the three arrows at the top of the figures indicate (*i*) time at which solution potential of the slowly stressed plants was lowered to -0.5 MPa, (*ii*) time at which solution potential of the slowly stressed plants was lowered to -1.0 MPa, and (*iii*) time at which solution potential of both the slowly stressed and rapidly stressed plants was lowered to -1.3 MPa. From left to right, the different symbols and lines represent successive cohorts starting with the the oldest cohort and ending with the youngest.

TABLE 1. Deaths and births in the final census interval (days 57–67) expressed as a percentage of the number of leaves present at the start of the interval

Species	Treatment	Deaths (%)	Births (%)
B. inermis	Unstressed	19a (100)	35a (100)
	Slow stress	10b (53)	36a (103)
	Rapid stress	38c (200)	11b (31)
A. desertorum	Unstressed	40a (100)	31a (100)
	Slow stress	10b (25)	41b (132)
	Rapid stress	46a (115)	15c (48)
S. viridula	Unstressed	21a (100)	21a (100)
	Slow stress	32b (152)	0b (0)
	Rapid stress	44b (210)	5b (24)
A. dasystachyum	Unstressed	23a (100)	29a (100)
	Slow stress	7b (30)	33a (114)
	Rapid stress	55c (239)	6b (21)

NOTE: For a given species and variable, values followed by different letters are significantly different at $p < 0.05$. Values in parentheses are number of deaths or births relative to those for unstressed plants.

Gradual stress decreased birth rates in all four species, but the decline was largely temporary. Birth rates dropped sharply when water potential of the medium was lowered to -0.5 MPa and again when potential was reduced to -1.0 MPa. However, birth rates approached those of unstressed control plants shortly after each of these drops in water potential (Fig. 1). If differences among treatments in number of leaves are taken into consideration (Table 2), gradual stress had no lasting effect upon births in A. dasystachyum and B. inermis, and actually increased births in A. desertorum by the end of the experiment. Stipa viridula was the exception to this pattern: birth rate dropped to zero when water potential was reduced to -1.0 MPa and never recovered.

Gradual stress initially had little effect on death rate (Fig. 1). However, by the end of the experiment death rate in the gradual stress treatment had declined relative to that in the unstressed controls in all species except S. viridula. This decline was more marked in the case of A. desertorum and A. dasystachyum than in B. inermis. Death rate per plant increased with gradual stress in S. viridula after water potential of the medium was decreased to -1.0 MPa. The subsequent recovery in death rate per plant (Fig. 1) was due to the small number of leaves left alive; deaths expressed on a per leaf basis (Table 1) were still greater than those of unstressed controls by the end of the experiment.

Cohort specific survivorship

A comparison of survivorship patterns in rapidly stressed plants (Fig. 2), reveals that rapid stress had little effect on cohorts 1, 2 and 3 in B. inermis, A. desertorum, and A. dasystachyum, or on cohorts 1 and 2 in S. viridula. This was because survivorship was already very low in these cohorts when stress was imposed. Rapid stress decreased survivorship in cohorts 4, 5, and 6 in B. inermis, A. desertorum, and A. dasystachyum, and in cohorts 3, 4, and 5 in S. viridula. Aside from those cohorts where survivorship was already low, younger cohorts experienced less mortality than older cohorts.

Comparing slowly stressed plants to unstressed controls (Fig. 2) indicates that slow stress had little effect upon survivorship of cohorts 1 and 2 in A. desertorum, B. inermis, and A. dasystachyum. These leaves were fully mature at the time water stress was first imposed. Slow stress substantially increased survivorship in cohorts 3 and 4, which emerged
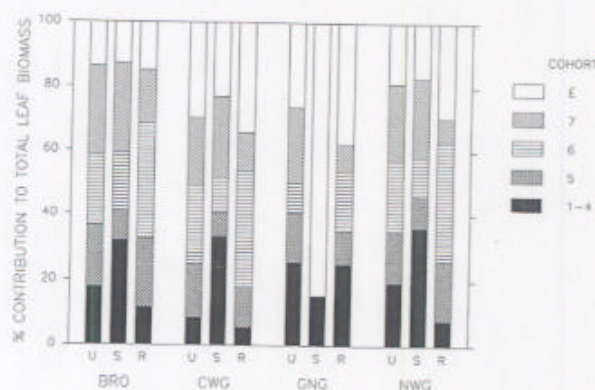

FIG. 3. Contribution of leaves of different ages to total leaf biomass for B. inermis, A. desertorum, S. viridula, and A. dasystachyum subjected to either no stress (U), slow stress (S), or rapid stress (R). Cohort 7 represents the youngest fully emerged leaves, and cohort 1 the oldest. Cohort E consists of those leaves not yet fully emerged at time of harvest.

immediately before and immediately after stress was first imposed. This effect was most marked in A. desertorum, followed by A. dasystachyum and B. inermis. There was also a tendency for slow stress to increase survival in cohorts 5 and 6, but by the final census, survivorship was high even in unstressed plants, so these effects were not large. Stipa viridula was different from the other species in that slow stress decreased survivorship. There was little difference among cohorts in the magnitude of this response; survivorship of all cohorts decreased substantially when subjected to water stress.

Age structure of leaf biomass

There were significant differences among species in age structure of the leaf biomass, and in how age structure was affected by water stress (as determined by MANOVA). Unstressed A. desertorum had a relatively young age structure: cohorts 1–4 were less important, and the emerging cohort more important, than in any of the other species (Fig. 3). Unstressed B. inermis and A. dasystachyum plants had similar age structures. The age structure of S. viridula was not significantly different from that of A. dasystachyum, but was different from that of B. inermis. The emerging cohort was more important in S. viridula than in B. inermis and cohort 6 was less important.

Rapid stress had roughly similar effects upon age structure in all four species, though the magnitude of the response varied (Fig. 3). Rapid stress decreased the importance of the cohort emerging at the time of stress (cohort 7), and increased the importance of the emerging cohort and cohort 6.

Slowly induced stress affected age structure in B. inermis, A. desertorum, and A. dasystachyum in a similar fashion. Older cohorts (1–4) increased in importance, middle-aged cohorts (5 and 6) decreased in importance, and younger cohorts (7 and E) were unaffected. Stipa viridula responded very differently to slow stress than the other species: the emerging cohort became the most important cohort, and all other cohorts except cohort 4 were eliminated.

The combined effects of differences among species and treatments in the importance of the various cohorts (with the

TABLE 2. Live leaf dry biomass and mean age of leaves ($\pm$ 1 SE) at harvest (day 67)

Species	Treatment	Live leaf biomass (g)	Mean age of leaves (days)
B. inermis	Unstressed	1.70 ± 0.24	16.0 ± 1.0
	Slow stress	0.87 ± 0.25	15.5 ± 1.1
	Rapid stress	0.89 ± 0.23	14.7 ± 1.0
A. desertorum	Unstressed	0.71 ± 0.13	13.4 ± 0.9
	Slow stress	0.54 ± 0.16	17.7 ± 1.1
	Rapid stress	0.65 ± 0.15	12.9 ± 1.1
S. viridula	Unstressed	0.15 ± 0.02	17.1 ± 1.1
	Slow stress	0.01 ± 0.03	25.2 ± 3.2
	Rapid stress	0.07 ± 0.01	21.2 ± 1.0
A. dasystachyum	Unstressed	0.68 ± 0.12	15.5 ± 1.0
	Slow stress	0.40 ± 0.10	18.1 ± 0.9
	Rapid stress	0.30 ± 0.12	14.9 ± 1.1

NOTE: Mean age of leaves was calculated by averaging the age of all leaf cohorts alive at day 67 after first weighting the cohorts by their biomass.

exception of the emerging cohort) is expressed in the mean age of leaf biomass (Table 2). In the no-stress treatment, the mean age of S. viridula was significantly greater than A. desertorum, A. dasystachyum, and B. inermis. Rapid stress had no effect upon mean leaf age in B. inermis, A. desertorum, and A. dasystachyum relative to the control. The changes in importance of both young and old cohorts caused by rapid stress (discussed earlier) tended to balance each other so that mean leaf age was not affected. Rapid stress caused mean leaf age in S. viridula to increase above that of the unstressed plants. Slow stress increased mean leaf age relative to the unstressed controls in all species except B. inermis (Table 2).

Leaf biomass

There were substantial differences among species in overall growth of the unstressed plants (Table 2). The largest leaf biomass was found in B. inermis and the lowest in S. viridula. Agropyron desertorum and A. dasystachyum were intermediate between B. inermis and S. viridula. Generally, the slow stress treatment had the lowest leaf biomass and the unstressed plants the highest (Table 2). The rapid stress treatment was usually intermediate between these two extremes. The species differed in the magnitude of this response, however. The differences among treatments in the two xeric species (A. desertorum and A. dasystachyum) were small relative to the differences among treatments for the two mesic species (B. inermis and S. viridula). Differences between gradually stressed and unstressed plants were significant at the 0.05 level in the case of both B. inermis and S. viridula and the difference between the rapidly stressed and unstressed plants was significant in S. viridula.

Discussion

Effect of slow verus rapid stress

Although both gradual and rapid stress reduced the number of leaves (Fig. 1) and final biomass (Table 2), the bases for the response varied. Rapid stress decreased birth rate and increased death rate, while the reduction in number of leaves with slow stress was due to reductions in birth rate; gradual stress actually increased leaf longevity (Fig. 2).

The contrasting effects of rapid versus gradual stress on leaf longevity can be attributed to acclimatory changes in gradually stressed leaves. Leaves developed under drought conditions generally exhibit small cell size, thick cell walls, small vacuoles, and high concentrations of solutes such as betaines and proline (Crawford 1989). These changes presumably allowed leaves in the gradual stress treatment to survive higher levels of stress than the unacclimated leaves of the rapid stress treatment. The oldest cohorts (1 and 2) exhibited little response to gradual stress (Fig. 2), indicating that young leaves were better able to acclimate.

Acclimation to water stress can explain why gradually induced stress did not increase leaf mortality, but does not explain why these leaves should live longer than unstressed leaves. Comstock and Ehleringer (1986) also found that leaf turnover is most rapid during periods of increased water availability. It appears that in general, periods of rapid growth are closely correlated with decreased leaf lifespan (Harper 1980). It has been suggested that plants are able to support only a limited number of leaves per shoot and that when conditions allow plants to develop leaves more quickly, this forces the death of old leaves by the removal of limited nutrients (Huiskes and Harper 1979).

Although water stress decreased birth rates, this effect in B. inermis, A. desertorum, and A. dasystachyum was only temporary (Fig. 1). Births in gradually stressed plants recovered at least partially shortly after each drop in water potential, and by the end of the experiment birth rates of gradually stressed plants either equalled or exceeded those of unstressed plants. The recovery in birth rates may be due to the accumulation of solutes and the positive effect this has on turgor and cell enlargement (Hsiao 1973; Morgan 1984) or on other processes such as hormone regulation (Munns 1988). Increased birth rates (relative to unstressed controls) may be due to the differential sensitivity of plant processes to water stress (Hsiao 1973). Cell elongation is more sensitive to stress than photosynthesis and cell division. Consequently, even though leaf elongation may cease when stress is first imposed, carbohydrate reserves accumulate and new leaves continue to be initiated, so that when leaf elongation is once again possible (i.e., after solute accumulation), there is a burst of growth (Kleinendorst 1975; Ludlow and Ng 1976, 1977; Chu et al. 1979; Horst and Nelson 1979).

The contrasting effects of rapid and gradual stress upon leaf age structure (Fig. 3; Table 2) is explained by the response of the various cohorts to the two types of stress. Rapidly stressed plants had a young leaf age structure because of the greater resistance of the younger cohorts to drought-induced mortality (Fig. 2), and the increased importance of the emerging cohort due to delays in emergence. Slowly stressed plants had an older leaf age structure because of the increase in leaf longevity with slow stress and the cumulative effect of reductions in birth rate over the period of stress. The different age structures suggest these two treatments will differ in their response to increased water availability. Plants subjected to a short period of rapid stress would respond quickly to increased water availability because of the high proportion of young, metabolically active tissue and its large bank of initiated but not yet emerged leaves. Plants subjected to the same level of stress gradually, over a longer period of time, would respond more slowly to increased water availability due to the lower photosynthetic activity of older leaves (Mooney et al. 1981; Miyaji 1986).

Differences among species in their response to stress

Based on the effect of water stress on number of leaves (Fig. 1), the ability to tolerate gradual stress was greatest in *A. desertorum* followed by *B. inermis*, *A. dasystachyum*, and *S. viridula*. Differences among species in ability to tolerate gradual stress were due to differences in the response of birth as well as death rates. Tolerant species exhibited a greater decrease in mortality and a better recovery of birth rates after stress than intolerant species (Table 1). The inverse correlation between mortality and the extent to which birth rates recover suggests a causal relationship. The extent to which birth rates recover after prolonged stress is probably dependent on maintenance of leaf area. Decreases in mortality would maintain the necessary leaf area to supply photosynthate for future growth.

Ability to tolerate gradual stress did not necessarily reflect ability to tolerate rapid stress. Based on number of leaves, there was no difference between *A. desertorum* and *B. inermis* in tolerance to rapid stress, and *A. dasystachyum* was actually less tolerant than *S. viridula*. The differential response of species to gradual versus rapid stress emphasizes the importance of considering the rate at which stress is imposed in assessing drought tolerance. Rate at which stress is imposed will vary both with climatic conditions and soil type. For example, water stress will develop more quickly on shallow, light-textured soils than on deep, heavy-textured soils. As a consequence, those characteristics that allow species to survive drought on shallow, course-textured soils are probably different from those on deep, heavy-textured soils.

The introduced species (*B. inermis* and *A. desertorum*) were more tolerant of both rapid and slow stress than native species (*S. viridula* and *A. dasystachyum*). In large part, this was due to the ability of these species to maintain birth rates in spite of stress (Table 1). The larger reductions in leaf growth in the native species would allow more resources to be allocated to root growth and thus ensure survival in the case of prolonged drought. The approach taken by the introduced species would result in greater productivity in the short term, but if stress were prolonged, could result in death of the plant.

The most striking example of tolerance to water stress was the absence of any effect of rapid stress on leaf mortality and the extent to which leaf longevity increased in response to gradual stress in *A. desertorum* (Table 1). The ability of *A. desertorum* to tolerate stress is probably related to its leaf age structure. The greater resistance of young leaves to stress (Fig. 2) and the young leaf age structure of *A. desertorum* (Fig. 3; Table 2) would result in less mortality. In this regard it should be noted that *S. viridula*, the species most sensitive to water stress, had the oldest leaf age structure (Table 2). Rate of leaf turnover and its effect on leaf age structure may well be a critical factor in the determination of a plant's ability to tolerate water stress.

Acknowledgements

BAZZAZ, F. A., and HARPER, J. L. 1977. Demographic analysis of the growth of *Linum ustitatissimum*. New Phytol. **78**: 193–208.

CHU, A. C. P., and McPHERSON, H. G. 1977. Sensitivity to desication of leaf extension in prairie grass. Aust. J. Plant Physiol. **4**: 381–387.

CHU, A. C. P., McPHERSON, H. G., and HALLIGAN, G. 1979. Recovery growth following water deficits of different duration in prairie grass. Aust. J. Plant Physiol. **6**: 255–263.

COMSTOCK, J., and EHLERINGER, J. 1986. Canopy dynamics and carbon gain in response to soil water availability in *Encelia Frutescens* Gray, a drought-deciduous shrub. Oecologia, **68**: 271–278.

CRAWFORD, R. M. M. 1989. Studies in plant survival: ecological case histories of plant adaptation to diversity. Blackwell Scientific Publications, Oxford.

GOUNOT, M., and YU, O. 1980. Research on the evaluation of aboveground net primary productivity of grassland Gramineae. Acta Oecol. Oecol. Plant. **1**: 81–102.

HARPER, J. L. 1980. Plant demography and ecological theory. Oikos, **35**: 244–253.

HARPER, J. L., and WHITE, J. 1974. The demography of plants. Annu. Rev. Ecol. Syst. **5**: 419–463.

HORST, G. L., and NELSON, C. J. 1979. Compensatory growth of tall fescue following drought. Agron. J. **71**: 559–563.

HSIAO, T. C. 1973. Plant responses to water stress. Annu. Rev. Plant Physiol. **24**: 519–570.

HUISKES, H. L., and HARPER, J. L. 1979. The demography of leaves and tillers of *Ammophila arenaria* in a dune sere. Oecol. Plant. **14**: 435–446.

HUNT, W. R. 1970. The influence of leaf death on the rate of accumulation of green herbage during pasture regrowth. J. Appl. Ecol. **7**: 41–50.

KAUFMANN, M. R., and ECKARD, A. N. 1971. Evolution of water stress control with polyethylene glycol by analysis of guttation. Plant Physiol. **47**: 453–456.

KLEINENDORST, A. 1975. An explosion of leaf growth after stress conditions. Neth. J. Agric. Sci. **23**: 139–144.

KNOWLES, R. P. 1987. Productivity of grass species in the dark brown soil zone of Saskatchewan. Can. J. Plant Sci. **67**: 719–725.

LOOMAN, J. 1983. 111 range and forage plants of the Canadian prairies. Agric. Can. Publ. No. 1751.

LUDLOW, M. M., and NG, T. T. 1976. Effect of water deficit on carbon dioxide exchange and leaf elongation rate of *Panicum maximum* var. *trichoglume*. Aust. J. Plant Physiol. **3**: 401–413.

—— 1977. Leaf elongation rate in *Panicum maximum* var. *trichoglume* following removal of water stress. Aust. J. Plant Physiol. **4**: 263–272.

MAJERUS, M. E. 1975. Response of root and shoot growth of three grass species to decrease in soil water potential. J. Range Manage. **28**: 473–476.

MAXWELL, J. O. 1977. A functional analysis of leaf growth and shoot production in *Agropyron*-dominated ecosystems. M.Sc. thesis, University of Saskatchewan, Saskatoon, Sask.

MICHEL, B. E. 1971. Further comaprisons between carbowax 6000 and mannitol as suppressants of cucumber hypocotyl elongation. Plant Physiol. **48**: 513–516.

MIYAJI, K. 1986. A new life table of leaves of *Phaseolus vulgaris* L. in relation to their position within the canopy and plant density. Ecol. Res. **1**: 303–322.

MOONEY, H. A., FIELD, C., GULMON, S. L., and BAZZAZ, F. A. 1981. Photosynthetic capacity in relation to leaf position in desert versus old-field annuals. Oecologia, **50**: 109–112.

MORGAN, J. M. 1984. Osmoregulation and water stress in higher plants. Annu. Rev. Plant Physiol. **35**: 299–319.

MUNNS, R. 1988. Why measure osmotic adjustment? Aust. J. Plant Physiol. **15**: 717–726.

PLAUT, Z., and FEDERMAN, E. 1985. A simple procedure to overcome glycol toxicity on whole plants. Plant Physiol. **79**: 559–561.