

Bunchgrass architecture, light interception, and water-use efficiency: assessment by fiber optic point quadrats and gas exchange

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Summary. The bunchgrass growth form, which is very prominent in water-limited environments, can result in considerable self-shading of photosynthetically active foliage. The consequences of this growth form for light interception and water-use efficiency (photosynthesis/transpiration, P/T) were investigated for two *Agropyron* species which differ in tussock density and degree of self-shading. During the period of most active gas exchange, the tussocks were very compact and photosynthesis of shaded foliage was markedly light-limited. Stomatal control of older shaded foliage was poorly attuned for water-use efficiency. At low light, P/T decreased and intercellular CO₂ concentrations increased. Despite differences in architecture and amount of shaded foliage, P/T of whole tussocks under ambient field conditions did not differ between these species. Partial defoliation decreased, rather than increased, P/T, primarily as a result of the poor photosynthetic light harvesting by the remaining foliage. Despite self-shading, the architecture of widely-spaced bunchgrasses provides for interception of as much direct beam solar radiation as is calculated for a rhizomatous grass occupying an area six-fold greater than the ground area underneath the canopy of these bunchgrasses.

Introduction

Grasses with a bunched or tussock growth form are prominent in steppe and desert regions of North America, Asia, Australia, Africa and South America (Schimper 1898; Moore 1964; Mack and Thompson 1982). The tillers of bunchgrasses are tightly clustered which can result in a very compact tussock and considerable self-shading of foliage. In contrast, rhizomatous grasses, such as in the water-limited short grass prairie, are considered to experience rather little self-shading (Knight 1973; Detling et al. 1978).

This paper explores the consequences of the bunched growth habit for light interception and the relationship between photosynthesis and transpiration, denoted as water-use efficiency. We compared two *C₃ Agropyron* bunchgrass species which differ in foliage density and arrangement, but whose leaf photosynthetic and stomatal conductance characteristics are similar (Caldwell et al. 1981). This assessment concentrates on the time of year when these grasses had developed substantial new foliage but before extensive internode elongation had taken place and the grass tussocks

were still in a very compact growth form (mid-April to end of May at this northern Utah site in western USA). The plants are most active in photosynthesis at this time since the foliage is still young and possesses high nitrogen concentrations. In addition, soil moisture is more abundant than later in the growing season and photosynthesis is not limited by excessive leaf temperatures or large vapor pressure differences between the foliage and air (Caldwell et al. 1981). Indeed, light may be the primary limiting factor for photosynthesis during this period.

Although removal of green foliage, such as by grazing animals, would generally be expected to decrease the photosynthetic capacity of the plant, it could result in a more favorable ratio between photosynthesis and transpiration, P/T, if photosynthesis of a significant portion of the tussock is light-limited due to shading.

Methods

Unlike a grass sward, bunchgrasses intercept solar radiation on the sides as well as top of the tussock. Interception of solar radiation by green foliage is a function of solar angle, foliage inclination and dispersion patterns and the arrangement of green and standing dead foliage of the tussock. The problem can be approached empirically by use of inclined point quadrats. Warren Wilson (1960, 1963, 1965 and 1967) has developed the theoretical basis for determination of canopy architecture and light penetration into vegetation. This theory can be extended to the question of light interception by isolated plants. Fiber optic point quadrats were employed in this study to increase accuracy and sampling speed (Caldwell et al. 1983). Foliage area of different plant parts of 11 bunchgrasses was determined by quadrats, inclined at 32°, during the period of 23 April to 24 May in 1981 and 1982 (Warren Wilson 1960, 1963, 1965). Projected areas of cylindrical parts were corrected to 1/2 the surface area of the cylinder. Two individuals of each species were intensively sampled both in 1981 and 1982 to determine foliage inclination at different heights in the tussocks by a combination of near vertical and horizontal quadrat samples. The variance in foliage angles was estimated independently from protractor measurements. These plants were also sampled to determine projected sunlit foliage at different solar angles corresponding to the position of the sun on May 20 for each hour of the day (List 1968). The projected sunlit green foliage was taken as the frequency of first contacts with green foliage. Al-

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though the geometry of these tussocks is assumed to be symmetrical with respect to azimuth angle, the intensive quadrat sampling was conducted at azimuth angles corresponding to the position of the sun at appropriate times of day.

Global (direct beam plus diffuse) solar photon flux density in the 400–700 nm waveband (termed photosynthetic photon flux density, PPFD) was measured by horizontally-mounted quantum sensors (Li-Cor Co. Lincoln, Nebraska) above and at the center of the base of bunchgrasses to assess light penetration into these tussocks. These sensors were interrogated every 10 s by a computerized data acquisition system and 1/2-h averages were calculated. Direct PPFD striking a plane normal to the solar beam was computed from ratios of global PPFD/total shortwave irradiation striking a horizontal plane as measured by a Stern pyranometer, and the calculated normally-incident direct beam total shortwave radiation. This normally-incident flux was derived using a pair of Stern pyranometers, one of which was equipped with a shadow ring. With corrections for the portion of the sky radiation blocked by the shadow ring, this pyranometer provided a measure of diffuse total shortwave radiation. Direct beam reaching a horizontal plane was derived by subtraction (Coulson 1975). Direct beam flux normal to the solar beam was then calculated from cosine law corrections. The ratio of direct beam to diffuse total shortwave radiation was assumed to apply to PPFD. Diffuse PPFD striking a plane normal to the solar beam was calculated from diffuse PPFD striking a horizontal plane assuming an isotropic hemisphere (Burt and Luther 1979). Shortwave and PPFD measurements were taken for several clear days in May of 1982 and calculations are appropriate to solar angles as would occur on May 20.

Simultaneous measurements of CO₂ and water vapor flux of individual leaf blades were made in situ on several dates from mid-April to the end of May. The dependency of net photosynthesis on PPFD for leaf blades near the bottom and the top of the tussock canopies was determined at a leaf temperature of 21°C, vapor pressure difference between leaf and air of 2.3 ± 0.3 kPa and near ambient air CO₂ concentrations. From the gas exchange data, leaf diffusive conductances and leaf intercellular CO₂ concentrations were also calculated. Carbon dioxide and water vapor exchange of individual foliage elements was measured on intact plants in the field with a CO₂ and H₂O vapor exchange porometer (Bingham and Coyne 1977). For the PPFD dependency relationships, either neutral density filters with solar radiation or an incandescent light source was employed.

Carbon dioxide and water vapor gas exchange of whole plants was also determined on several dates during this period with a large cuvette system programmed to track ambient conditions of temperature and vapor pressure deficit as the plants were exposed to solar radiation on primarily cloudless days. A measurement series was also conducted following partial defoliation of bunchgrass plants. The semi-cylindrical configuration of the chamber allowed solar radiation to impinge on the plants from all azimuth angles except from the north, where the Peltier heat exchanger was located. The heat exchanger and electronic control system were modified from an original Sirigor (Siemens Co., Erlangen, West Germany) chamber (Koch et al. 1971). Regulated flow rates up to 100 l min⁻¹ can be accommodated

in this chamber. Incoming air was partially dehumidified using a heatless dryer (Puregas Co.) so that outgoing vapor concentrations approximated those of the ambient air. In all but three dates in 1981, air flow from the cuvette to the infrared gas analyzer was transported in stainless steel tubing to minimize water vapor and CO₂ adsorption. Further details of this system are contained in Caldwell et al. (1981).

Gas exchange calculations for both the CO₂–H₂O porometer and the whole-tussock cuvette systems included correction factors recommended by von Caemmerer and Farquhar (1981) to take into account dilution of the air stream by transpiration and interactions of gasses in calculation of conductances.

A description of the *Agropyron* bunchgrass species, the study area and climate in northern Utah is contained in Caldwell et al. (1981).

Results

The architecture of the two *Agropyron* bunchgrasses for the period of the growing season when these tussocks are most compact is shown in Fig. 1. This is a composite diagram of the 11 bunchgrass plants sampled during a 31-day period (23 April–24 May) in 1981 and 1982. Individual plant size varied and the plants were rapidly growing during this period of active photosynthesis. The average total green foliage area of *Agropyron desertorum* (Fisch. ex Link) Schult. was 1,920 cm² (standard error, S.E., 410 cm²) and 1,240 cm² (S. E., 135 cm²) for *Agropyron spicatum* (Pursh) Scribn. and Smith. (A proposed taxonomic revision (Dewey 1983) will change this name to *Elytrigia spicata* (Pursh) D.R. Dewey.) The green stem area accounted for only 2% of the total green foliage area of *A. spicatum* and less than 0.5% for *A. desertorum*. The primary differences between these species were that *A. desertorum* had greater foliage area and canopy denseness while *A. spicatum* had greater variance of foliage angle distribution. Destructive harvests

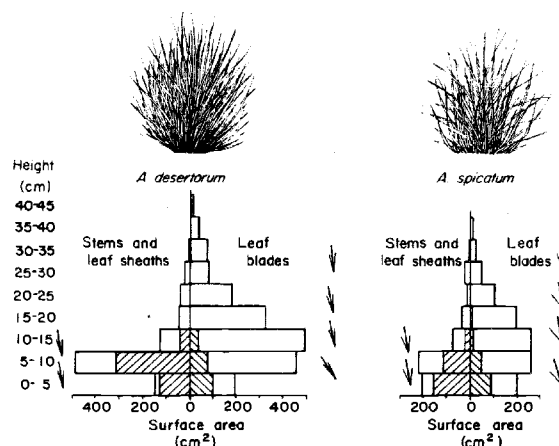


Fig. 1. Composite depictions of leaf blade, leaf sheath and stem area distributions with height for bunchgrasses of *A. desertorum* and *A. spicatum* during the season when these grasses are most compact. This composite is based on 6 *A. desertorum* and 5 *A. spicatum* plants intensively sampled between April 23–May 24 in 1981 and 1982. The hatched portion of the histograms indicates dead or senescent foliage. Average foliage inclination angles and their standard deviations are indicated for different heights of the tussocks for both leaf blades and sheaths

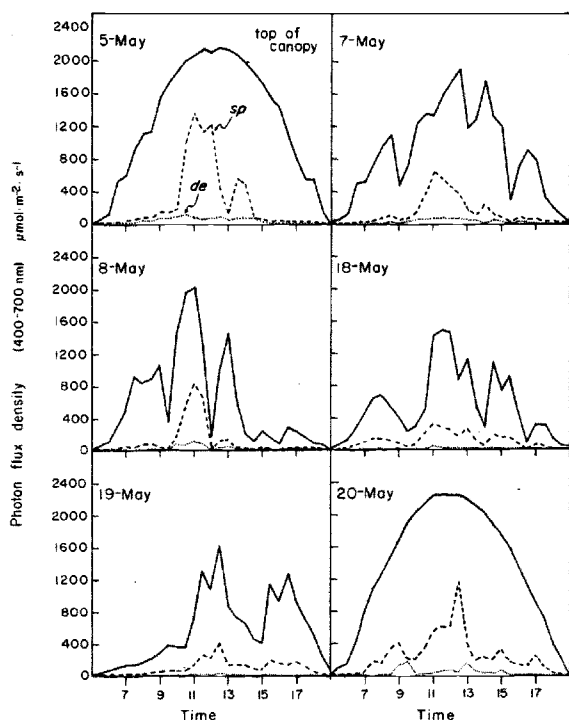


Fig. 2. Measurements of photon flux density (400–700 nm) at the top and at the base of tussocks of *A. desertorum* (de) and *A. spicatum* (sp) on several days in 1982. The quantum sensors were horizontally mounted. The irradiance is plotted as 1/2-h averages as a function of true solar time

of other plants in this study have also indicated that *A. spicatum* tends to have about 20% more green foliage area per tiller than *A. desertorum*. Therefore, the total green foliage area in tussocks of *A. spicatum* is distributed on fewer tillers than in *A. desertorum*. These differences result in a more open-structured tussock for *A. spicatum*.

The differences in these two species are also indicated by measurements of PPFd at the tussock base (Fig. 2). Even on cloudless days, PPFd at the base of the *A. desertorum* tussock exceeded only $50 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for 4 to 5 h per day and usually did not exceed $100 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ for more than a 1/2-h period. In contrast, PPFd at the base of the *A. spicatum* tussock on cloudless days could exceed $1,000 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ and was always greater than in *A. desertorum* under all conditions. The quantum sensors at the base of the tussocks were adjacent to green, photosynthetically-active foliage. Because the values shown in Fig. 2 are averages over 1/2-h periods, short-duration sun flecks would be integrated into these 1/2-h values. On a daily basis, total photon flux reaching green foliage at the bottom of *A. spicatum* tussocks ranged from 17 to 22% of that at the top of the tussock for the days depicted in Fig. 2, while in the *A. desertorum* tussock total daily photon flux was always less than 5% of that reaching the top of the tussock. While it is evident from these measurements that considerable self-shading of foliage in the tussocks occurs, a quantitative depiction of light interception by whole tussocks is better represented by the point quadrat sampling.

The projected area of green foliage in the direction of the solar beam during the course of a cloudless day is given

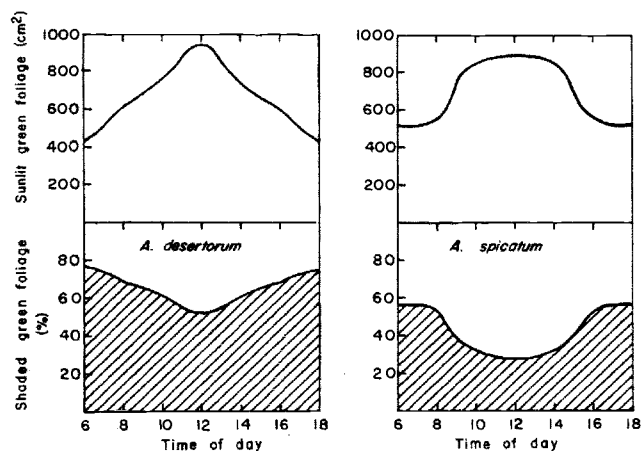


Fig. 3. Projected area of green foliage intercepting direct beam solar radiation for the plants depicted in Fig. 1 for solar angles as would occur on May 20 at latitude 42°N . The percentage of green foliage area in shade is also shown. Time of day is true solar time

in Fig. 3 for solar angles appropriate to May 20 at this location. This is calculated for the composite plant architectures depicted in Fig. 1 and based on the intensive point quadrat sampling at angles corresponding to the solar beam at each hour of the day. Although the total green foliage area of *A. desertorum* is 50% greater than for *A. spicatum*, the projected sunlit foliage area during much of the day is about the same for the two species. The percentage of shaded foliage, calculated as the difference between total green foliage area and projected sunlit foliage area, is greater for *A. desertorum*. This calculation of shaded foliage corresponds in magnitude with that calculated from total and initial contact frequencies at three different quadrat angles. However, due to light scattering and penumbral effects, there is not always a sharp distinction between sunlit and shaded foliage as depicted here, especially in the interior of the tussock. Nevertheless, *A. desertorum* has a greater proportion of foliage that is not receiving direct beam radiation.

For widely-spaced bunchgrass plants, the direct beam irradiance from all angles impinging on sides and top of the tussock should be considered. Normally-incident solar direct photon flux density (400–700 nm), PPFd, is presented in Fig. 4 (top) for solar angles appropriate to May 20. The diffuse PPFd incident on a similarly-inclined surface is also presented for perspective. The total direct beam photon flux intercepted by green foliage of the plants portrayed in Figs. 1 and 3 is also depicted in Fig. 4 (bottom). This is the product of normally-incident PPFd and projected sunlit green foliage area for solar angles appropriate to May 20. The total direct beam and diffuse photon flux received on a level plane equivalent in area to the ground beneath the canopy crown of an average tussock (27 cm diam.) is also shown for perspective.

Net photosynthesis, diffusive leaf conductance for water vapor, g_w , and leaf intercellular CO_2 concentration, c_i , are presented as a function of PPFd for individual leaf blades in Fig. 5. These are taken from a series of field measurements on intact leaves conducted throughout April and May in 1980 and 1981, and represent leaf blades near the base and near the top of the tussocks. Leaf blades at the base of the tillers were older and normally well shaded.

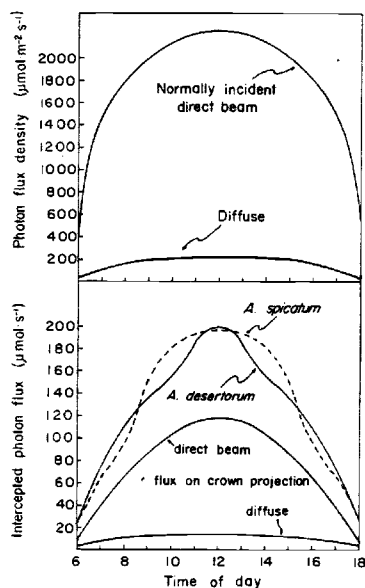


Fig. 4. Normally-incident solar direct beam photon flux density (400–700 nm) and diffuse photon flux density incident on a similarly-inclined surface for solar angles appropriate to May 20 at this site (top). Total direct beam photon flux intercepted by green foliage of the plants depicted in Figs. 1 and 3 and the direct beam and diffuse photon flux intercepted by level ground equivalent in area to the average canopy crown projection of these tussocks as a function of true solar time

Although the gas exchange behaviour of individual leaf blades of different tillers varied somewhat, older leaves at the base of the tillers had consistently lower photosynthetic rates and usually exhibited light saturation at much lower PPFD than blades near the top of the tussock. Leaf conductance, g_w , of older foliage was often, though not always, lower than that of young foliage. Conductance generally decreased with declining PPFD but not as rapidly as the decrease of photosynthesis. Consequently, c_i increased for almost all leaf blades at PPFD less than $800 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$. Thus, the photosynthesis/transpiration ratio, P/T , of shaded foliage would probably be much lower than for sunlit foliage, especially since shaded foliage is usually the older foliage on the tiller and g_w of older foliage is less responsive to PPFD changes than is g_w of younger foliage. The gas exchange characteristics of these two species were generally similar except that maximum photosynthetic rates of *A. spicatum* leaves at the top of the canopy were often greater and g_w of this species differed more between upper and lower leaves than in *A. desertorum*. Photosynthesis and transpiration of individual leaf blades taken under prevailing ambient conditions of PPFD, leaf temperature and vapor pressure difference between leaf and air showed that P/T ratios of shaded foliage were considerably lower than those of sunlit foliage (Fig. 6).

Because *A. desertorum* has a smaller proportion of its foliage directly exposed to the solar beam and foliage lying in deep shade exhibits very low P/T , tussocks of *A. desertorum* might be expected to have lower water-use efficiency

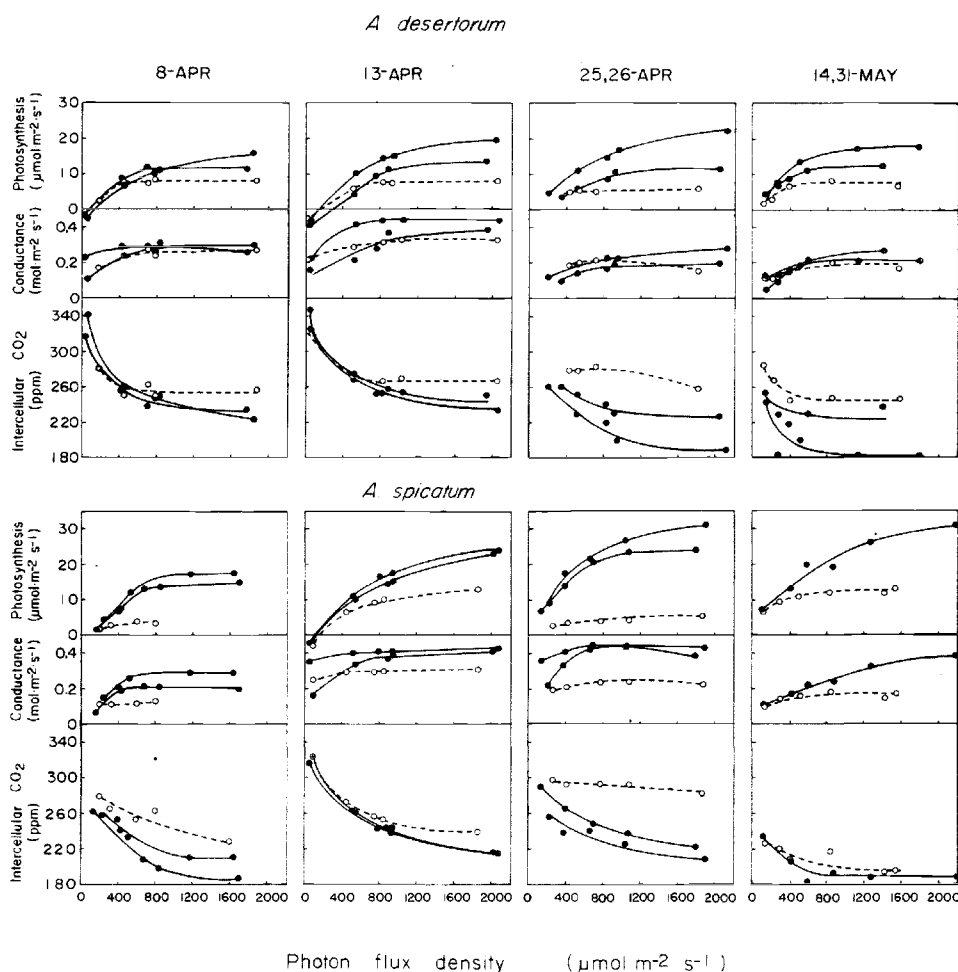


Fig. 5. Net photosynthesis, diffusive leaf conductance for water vapor and leaf intercellular CO_2 concentrations as a function of photon flux density for leaves of individual bunchgrass tillers on different dates in 1980 and 1981. The dashed lines and open circles represent older leaf blades near the base of the tussocks while the solid lines and closed circles are for the two leaves of the same tillers near the top of the tussocks

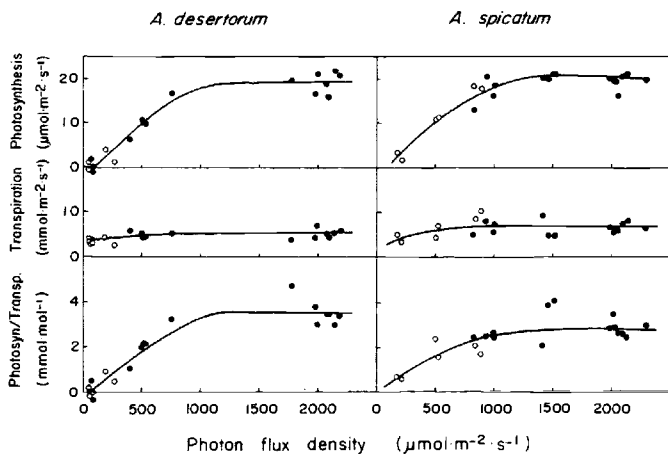


Fig. 6. Net photosynthesis and transpiration of individual leaf blades measured under prevailing ambient conditions of leaf temperature, vapor pressure difference between leaf and air, and photon flux density. These measurements were collected for leaves at different heights in the tussock. Open circles represent the oldest green leaf blades on individual tillers at the base of the tussock and the other data points represent younger leaf blades at higher locations in the tussocks. These measurements were taken during the middle 5-h of the day on May 13, 20 in 1982. Leaf temperatures ranged between 12 and 24° and vapor pressure difference between leaf and air was in the range of 1.0 to 2.6 kPa

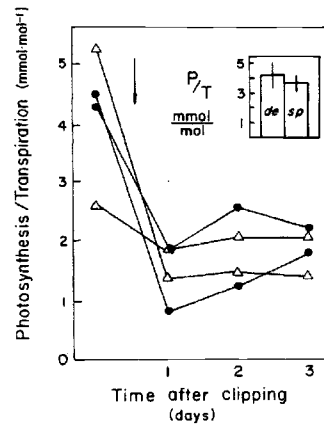


Fig. 7. Daily integrated ratios of photosynthesis/transpiration measured for whole bunchgrasses with the large gas exchange cuvette system tracking ambient environmental conditions during the period from mid-April to mid-June in 1981 and 1982. All measurements were taken during days of minimum cloud cover. The arrow indicates the time of partial defoliation of 4 plants (open triangles, *A. spicatum*, closed circles, *A. desertorum*) and the time following partial defoliation represents measurements of daily gas exchange during primarily cloudless days. In the inset are average and standard deviations of daily P/T ratios of 11 tussocks not subjected to defoliation during this period of time

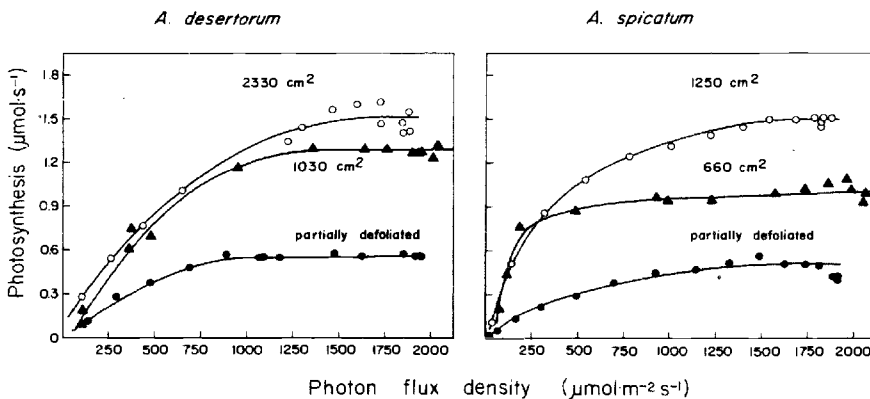


Fig. 8. The relationship between daily net photosynthesis of entire bunchgrasses as a function of photon flux density for bunchgrasses of different size. These data were collected during the afternoon periods (April 29–May 4, 1981 and 1982) on cloudless days when the large cuvette system was tracking ambient environmental conditions. The green foliage area of each plant is indicated. Also shown are the same relationships for the second cloudless day following partial defoliation of tussocks in mid-May, 1982. Foliage temperatures were between 17 to 27° C which is within the optimal range for photosynthesis at this time of year

over the course of a day than *A. spicatum*. It might also be expected from these individual leaf measurements that partial defoliation of either species could improve water-use efficiency because of reduced self-shading. However, it should be emphasized that water-use efficiency of entire tussocks depends on the quantitative contribution of foliage of different physiological states in different microenvironments in the tussock. Much of the sunlit foliage is younger, more photosynthetically-active tissue and gas exchange of this foliage may overwhelm that of older, shaded foliage. This is borne out by gas exchange measurements of whole bunchgrasses over several days in the late April–May period when the large cuvette system was tracking ambient environmental conditions (Fig. 7). These measurements indicated that the two species did not differ in water-use efficiency and further showed that partial defoliation of either species always resulted in decreased water-use efficiency. Approximately 60 to 85% of the green foliage area was removed in these partial defoliations.

An indication of photosynthetic light harvesting by

these bunchgrasses under ambient conditions can be gleaned from the relationship between photosynthesis of the whole tussock and PPFD. Such relationships are plotted for tussocks of quite different size and also for partially defoliated tussocks in Fig. 8 (these are from the measurement series included in Fig. 7). Smaller tussocks underwent apparent light saturation at lower PPFD, whereas, larger bunchgrasses exhibited increasing tussock photosynthetic rates at higher PPFD. In this case, however, an *A. spicatum* of 1,250 cm² foliage area apparently can harvest as much light as an *A. desertorum* with 2,330 cm² foliage area. The partially defoliated plants exhibited very little increase of photosynthesis above a PPFD of 750 µmol quanta·m⁻²·s⁻¹. At this time of year, the partially defoliated bunchgrasses would be essentially light saturated for the middle 9 h of the day. This apparent light saturation was not the result of excessive leaf temperature because foliage temperatures were in the range of 17–27°, which are in the optimal range for photosynthesis of these species at this time of year (Nowak, unpublished data).

Discussion

Photosynthetic light harvesting by these *Agropyron* bunchgrasses is dependent on size of tussock as well as environmental conditions; however, it appears that at least under certain conditions an *A. spicatum* tussock is able to harvest the same amount of light as an *A. desertorum* tussock which has 80% more green foliage area (Fig. 8). This may be attributed both to the architecture and photosynthetic characteristics of these species. The green foliage of an *A. spicatum* tussock can intercept as much direct beam light as that of an *A. desertorum* tussock which has approximately 50% more total green foliage area (Fig. 4). In addition, the most photosynthetically active leaves of *A. spicatum* often have higher photosynthetic rates per unit foliage area than those of *A. desertorum* (Fig. 5, Caldwell et al. 1981). Each species likely has an optimal tussock size for light harvesting under particular conditions; however, more data would be required to test this proposition.

The differences in these species may reflect the different herbivory pressures received during their evolutionary history. *Agropyron desertorum* is a Eurasian species which has been naturalized in North America and in its native environment evolved in the presence of large populations of ungulates. Thus, it likely encountered a greater probability of defoliation than *A. spicatum* which is native to the Intermountain West of North America where few large herbivorous mammals have existed, at least since the Pleistocene (Mack and Thompson 1982; Caldwell et al. 1981). In its native environment, the *A. desertorum* tussocks may have been typically grazed and thus at least partially defoliated. Consequently, without herbivory, *A. desertorum* has a greater proportion of shaded green foliage than *A. spicatum* (Fig. 3) and some of this foliage can be in a very low light environment even on cloudless days (Fig. 2).

The question can be raised as to whether *A. desertorum* without some foliage removal may have tussocks which are too dense, especially for efficient use of water. The P/T of light-limited foliage depends on the stomatal behavior of shaded foliage elements. Until photosynthesis becomes severely light-limited, a reduction of g_w in response to decreasing light that is proportional to the decline of photosynthesis can reduce transpiration and yet maintain a constant c_i . Thus, if these shaded leaves maintain a positive carbon balance and P/T similar to those of other foliage on the plant, this shaded foliage would still be an asset to the tussock. The very shaded foliage elements of both bunchgrass species are primarily the older leaves which exhibit reduced photosynthetic capacity and saturation of photosynthesis at low PPFD. These photosynthetic characteristics may in part be the result of a shade adaptation and in part simply the result of advanced leaf age (Field 1981). These older leaves did not, however, exhibit efficient curtailment of g_w at low PPFD (Figs. 5 and 6). Instead, under light-limiting conditions, c_i increased and P/T tended to decrease. Although, this may be a general characteristic of older foliage (Turner 1974) it has not been well documented in the literature.

Extrapolation of information on canopy architecture, the light environment within tussocks, and individual leaf gas exchange behavior (Figs. 2, 3, 5 and 6) to gas exchange of whole tussocks would suggest that *A. desertorum* should exhibit lower water-use efficiency than *A. spicatum* under field conditions when photosynthesis is not otherwise lim-

ited by environmental factors such as excessive leaf temperatures or water stress. However, such differences were not apparent in the series of gas exchange measurements of whole tussocks in the field (Fig. 7 inset). Under these conditions, the proportional contribution of the more physiologically active, well-illuminated foliage to gas exchange of the entire tussock outweighed differences between these species in the proportion of shaded foliage with reduced P/T. Although it is common in ecophysiological studies to extrapolate from individual leaf gas exchange activity to behavior of the whole plant, such extrapolations present a formidable sampling problem (e.g., Leverenz et al. 1982). This underscores the importance of gas exchange measurements of whole plants or larger subunits of plants under field conditions whenever feasible.

Partial defoliation of compact bunchgrasses with a significant amount of light-limited foliage hypothetically could result in increased P/T even though total tussock photosynthesis would be reduced. However, gas exchange measurements of whole tussocks in the field clearly did not support this proposition (Fig. 7). Photosynthesis/transpiration ratios sharply declined following partial defoliation and though total tussock photosynthesis slowly increased in succeeding days, P/T remained low. The tussocks in these experiments were defoliated to the extent that there was practically no self-shading within the tussock. The majority of foliage removed from these bunchgrasses was in the category of young, upper leaf blades and leaf sheaths which were the most photosynthetically active foliage elements (Fig. 5). This type of foliage is preferentially eaten by livestock when these plants are in this growth stage (P. Johnson, personal communication). Consequently, the remaining foliage is older, less photosynthetically active material. The net result was that the P/T of the tussock was reduced.

Photosynthetic harvesting of solar radiation by these partially defoliated tussocks was not efficient. Only a slight increase of photosynthesis occurred when PPFD increased above $750 \mu\text{mol quanta} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ (Fig. 8). Thus, for clear days at this time of year, the tussocks were effectively light-saturated for the middle 9 h of the day. Although partial defoliation clearly did not result in increased P/T, it is plausible that a different pattern of defoliation could result in an increase of water-use efficiency. For example, insect herbivores might remove foliage on the plant in a pattern which could reduce the amount of shaded foliage without a disproportionate loss of the most productive foliage elements.

Even if water-use efficiency were increased by a particular pattern of partial defoliation, the benefits might be questionable. In this environment, soil moisture, and likely mineral nutrient resources, are most dependably available to the plants at this time of year (mid-April to end of May) (Caldwell et al. 1981). Vapor pressure differences between foliage and the atmosphere in these experiments seldom exceeded 2 kPa and, thus, would be very conducive to high P/T. Leaf temperatures seldom exceeded 25° and were generally in the optimum range for photosynthesis (Nowak, unpublished data). Indeed, total day P/T values are as high as have been reported for plants in arid environments (Lange et al. 1969, Hellmuth 1971; Caldwell et al. 1977). If partial defoliation did improve water use efficiency, the rate of water use by these tussocks also would be reduced because of less transpiring foliage. Postponement of this moisture resource use to later in the year when the higher atmospheric stress is much less conducive to high P/T could

more than offset the improved P/T earlier in the season due to partial defoliation. Furthermore, postponement of resource use could result in surrendering some of this resource to neighboring plants.

Widely-spaced bunchgrasses in water-limited environments constitute islands of compact foliage. When calculated on the basis of ground area beneath the canopy of these grasses, the composite plants depicted in Fig. 1 would have green foliage area indices (foliage area/ground area) of 3.4 and 2.2 for *A. desertorum* and *A. spicatum*, respectively (assuming an average canopy crown projection of 27 cm diameter). In contrast, in the short grass prairie, an environment of similar annual precipitation and evaporative demand, the maximum green foliage area index is 0.5 (Knight 1973). Though considerable self-shading occurs in these bunchgrass islands, the total daily interception of photon flux by green foliage of these tussocks may not be so much different than that received by a rhizomatous grass with little self-shading. Because the tussocks receive solar radiation on the sides as well as the top of the tussock, the total direct beam photon flux received during the course of a day could be equivalent to that received on a level ground area some 70% greater than the canopy crown projection of these tussocks (Fig. 4).

It is possible to compute the total intercepted direct beam photon flux that would impinge on a rhizomatous grass assuming a foliage area index of 0.5, foliage inclination angles the same as those of the bunchgrasses, and randomly distributed foliage elements from the theory developed by Warren Wilson (1967). If this is done for solar angles and radiation conditions as depicted in Fig. 4, a rhizomatous grass of these characteristics would need to occupy an area 6.4 times that of the ground area under the canopy crown projection of these bunchgrasses in order to intercept the same total direct beam flux. However, the diurnal course of intercepted direct beam photon flux would be different for the rhizomatous and tussock grasses with proportionately more radiation being intercepted in the mid-portion of the day by the bunchgrasses. Interestingly, if the green foliage area of these bunchgrasses as portrayed in Fig. 1 were dispersed as randomly arranged foliage over this 6.4-fold greater ground area, they would have foliage area indices of 0.53 and 0.34 for *A. desertorum* and *A. spicatum*, respectively.

The selective advantages of the bunchgrass growth habit probably lie with factors other than display of foliage to solar radiation. These may involve fire tolerance, reduction of the extent of grazing, competitive position and space occupation, etc. These factors are presently, however, largely a matter of speculation. While the bunchgrass growth habit may not necessarily represent optimal architecture for light interception, photosynthetic light harvesting and water use efficiency, this analysis suggests that these bunchgrasses are not so inefficient in this regard. Furthermore, for partial defoliation to improve water use efficiency, it would need to be executed very selectively with respect to age and position of foliage elements within the tussock.

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