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Gas Exchange and Water Relations of Two Alpine and Two Arctic Tundra Plant Species

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GAS EXCHANGE AND WATER RELATIONS OF TWO ALPINE AND TWO ARCTIC TUNDRA PLANT SPECIES

by

Douglas Allan Johnson

A dissertation submitted in partial fulfillment
of the requirements for the degree

of

DOCTOR OF PHILOSOPHY

IN

Range Ecology

Approved:

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1975

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Douglas Allan Johnson

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ABSTRACT

Gas Exchange and Water Relations of
Two Alpine and Two Arctic Tundra
Plant Species

by

Douglas Allan Johnson, Doctor of Philosophy

Utah State University, 1975

Major Professor: Martyn M. Caldwell
Department: Range Ecology

Although water stress is an important selective force in many environments, it is not commonly considered to be of particular importance in tundra areas. Even though large portions of tundra may have an abundance of water, other more exposed areas may become quite dry. This microsite variability with respect to moisture stress was reflected in soil water potential measurements obtained from an alpine tundra area on Niwot Ridge in Colorado. Even though soil water potentials were consistently above -5 bars in a relatively low lying <u>Deschampsia</u> meadow, soil water potentials from an exposed fellfield area were often as low as -15 bars.

Since moisture stress affects a number of important physiological processes in plants and since moisture stress may develop in at least some tundra areas, this study was undertaken to determine whether the sensitivity of plant physiological processes

to water stress may be one important contributing factor in determining the microsite distribution of different tundra species. The alpine tundra species examined in this study were *Deschampsia caespitosa* which is typically found in wet meadow habitats and *Geum rossii*, a species which ranges from wet meadow to exposed fellfield habitats. The arctic tundra species investigated were *Dupontia fischeri* which is restricted mainly to wet meadow areas and *Carex aquatilis*, a species ranging from wet meadows to drier, more exposed areas.

For both the arctic and alpine tundra species, though the photosynthetic capacities of the tundra species restricted mainly to wet meadow areas were higher under conditions of low moisture stress, the wider ranging tundra species were able to maintain greater photosynthetic capacity as soil moisture stress increased. Although the depression of photosynthesis with water stress in these tundra species could be partially attributed to reduced stomatal aperture, with decreased soil water potential most of the decline of photosynthesis was due to a greater non-stomatal or residual resistance, indicating a direct impact of water stress on the photosynthetic apparatus. Dark respiration did not increase with enhanced water stress. Thus, although photorespiration may have increased, increased mitochondrial respiration is unlikely involved in the depression of net photosynthesis. The wet site species typically exhibited higher photosynthesis/transpiration ratios for photosynthesis at low soil moisture stress levels;

however, as soil moisture stress increased, the wider ranging species generally maintained higher photosynthesis/transpiration ratios.

At high soil water potentials stomata of the species restricted typically to wet meadow tundra areas did not appear to undergo a closing response until the bulk leaf water potential decreased; however, reduced stomatal aperture of the tundra species with a wider distribution was noted before leaf water potential dropped. Although the stomatal mechanism of wet site tundra species exhibited lower degrees of occlusion at high soil water potentials, for the more widely distributed tundra species, Carex and especially Geum, stomatal closure was less pronounced as soil water potential decreased.

The ability of Geum to maintain a low liquid phase water transfer resistance from the soil to the leaves as well as to experience relatively small reductions in turgor pressure as moisture stress increased may be important factors in maintaining a favorable leaf water balance over a rather broad range of soil moisture regimes. Differences in turgor pressure response with respect to moisture stress may be associated with differences in cell wall elasticity. Calculations of cell wall elasticity suggest that the wider ranging species have more elastic cell walls as compared with the more rigid, inelastic cell walls in the wet site tundra species. The results of this study show that tundra plants have different gas exchange sensitivities and water relation responses with respect to moisture stress and suggest that these attributes may be important contributing factors in determining the local distribution of these species.

(137 pages)

CHAPTER I

INTRODUCTION

Although tundra systems have been of special interest for a number of years, integrated studies of tundra systems have been only recently undertaken (Bliss, 1972; Wielgolaski and Rosswall, 1972; Bliss et al., 1973). This renewed interest in tundra ecosystems has occurred largely because of the recent discoveries of vast, unexploited, nonrenewable resources in Alaska, Canada, and Siberia. An understanding of the adaptive mechanisms of native tundra species is a necessary requisite for the wise technological development of these especially fragile ecosystems.

Tundra is a Russian-derived word meaning marshy plain. However, more recently tundra has come to refer to an ecosystem characterized by treeless landscapes beyond timberline. Basically there are two types of tundra: 1) arctic tundra and 2) alpine tundra. Arctic tundra refers to treeless landscapes latitudinally beyond timberline, while alpine tundra refers to treeless landscapes above timberline. Whittaker (1970) estimates that arctic and alpine tundra systems occupy about 8 million km^2 or approximately 5 percent of the earth's land surface. The circumboreal arctic tundra belt comprises clearly the largest portion of tundra with the rest consisting of relatively small, isolated alpine tundra areas.

Arctic and alpine tundras differ as to the number and kinds of plant species which make up their vegetation. As Billings (1973) states, there is a general attenuation in floristic richness as one proceeds from the mid-latitude alpine tundras to the arctic tundras. For instance, Munz and Keck (1959) list 615 alpine plant species for the Sierra Nevada Mountains, while Bamberg and Major (1968) report 291 species from three Montana mountain ranges. Contrastingly, Bliss (1971) reported only 111 plant species for the Arctic Archipelago while Tolmachev (1966) reported 118 species on the Taimyr Peninsula. Thus, even though the areal extent of the alpine tundra is less than the arctic tundra, their floras contain a larger number of species. Billings (1973) suggests that these differences may be due to differences in diversity of habitats, relative age, and their glacial history.

Even though arctic and alpine tundras differ as to the number and kinds of species which make up their vegetation, tundra plant communities can generally be characterized as consisting predominantly of low-growing perennial herbs, dwarf shrubs, lichens, and mosses. Annuals in tundra environments are extremely rare (Sorenson, 1941; Porsild, 1964; Mark and Bliss, 1970). Bliss (1971) suggests that tundra environments with their general lack of heat in the short summer are not conducive to the evolution of annuals which require considerable heat for maturity and seed set. Detailed descriptions of vegetation patterns, composition, and structure of arctic vegetation can be found in Polunin (1948), Hanson (1953), Britton (1957), Larsen (1965), Caldwell, Tieszen and Fareed (1974), and Löve and Löve (1974). Similar descriptions for alpine vegetation are contained in Braun-Blanquet (1948), Troll (1957), Billings and

Table 1. Comparative environmental characteristics of an arctic tundra location at Barrow, Alaska (71°20'N, 156°46'W, 3 m elev.), and an alpine tundra location on Niwot Ridge (40°04'N, 105°36'W, 3476 m elev.) in Colorado (from Billings and Mooney, 1968).

Environmental Characteristic	Arctic Tundra	Alpine Tundra
Growing days	60 to 90	60 to 90
Maximum photoperiod	84 days	15 hr
Air temperature, July mean (+1 m, °C)	3.9	8.3
Soil temperature, absolute maximum (-15 cm, °C)	2.5	13.3
Wind, annual mean ($km \cdot hr^{-1}$)	19.3	29.6
Solar radiation		
Mean July intensity ($cal \cdot cm^{-2} \cdot min^{-1}$)	0.30	0.56
Mean July total (langleys)	426	497
Precipitation, annual mean (mm)	107	634

the winter months, annual mean precipitation in the arctic tundra is markedly lower than that received in the alpine tundra.

The annual aboveground productivity in tundra ecosystems has been reviewed by Bliss (1962, 1970) and Bliss et al. (1973) and ranges between 3 to 242 $g \cdot m^{-2}$ (Bliss, 1956; Warren Wilson, 1957; Dennis and Johnson, 1970; Tieszen, 1972; Wien and Bliss, 1974). Bliss (1966) and Webber (1974) indicate that tundra plant productivity when expressed on a growing season basis is quite comparable to other natural systems.

A very high proportion of tundra plant biomass lies belowground (Scott and Billings, 1964; Bliss, 1966; Mooney and Billings, 1968; Alexandrova, 1970; Dennis and Johnson, 1970). For instance, Dennis and Johnson (1970) found as much as 98 percent of the living plant material may be beneath the soil surface in the form of roots and rhizomes in an arctic tundra community. Similarly, results of Scott and Billings (1964) indicate that over 79 percent of the total standing crop of vegetation was belowground in alpine tundra plants. These belowground storage compartments allow carbohydrate storage throughout the winter. Data of Mooney and Billings (1960) and Fonda and Bliss (1966) indicate that the spring burst of regrowth following snowmelt occurs at the expense of these underground root and rhizome reserves. In addition, Billings (1973) suggests that these high belowground-to-aboveground ratios may be important for water and mineral uptake in the cold tundra soils.

Another characteristic of tundra vegetation is its high caloric content (Golley, 1961; Bliss, 1962; Jordan, 1971). Hadley and

Bliss (1964) have found that the high caloric content of some tundra plants may be a result of high lipid content; however, most food storage seems to be in the form of carbohydrates contained in below-ground structures. Jordan (1971) suggests that the adaptive advantage of these high caloric contents may be that less energy is spent processing a concentrated food source. This seems to correspond well with the rapid leaf expansion which occurs in tundra plants (Billings and Bliss, 1959; Johnson and Caldwell, 1974). More detailed coverage on the adaptations of tundra plants is contained in Billings and Mooney (1968), Johnson (1969), Bliss (1971), Savile (1972), Billings (1974), and Tieszen and Wieland (in press).

In tundra plants, as well as plants in other ecosystems, long-term survival is strongly hinged on the ability of these plants to fix and utilize energy. Even though tundra areas are relatively remote and inaccessible, a number of field photosynthetic studies have been conducted in tundra environments (Mooney and Billings, 1961; Mooney, Wright, and Strain, 1962; Hadley and Bliss, 1964; Billings, Clebsch and Mooney, 1966; Tieszen, 1973; Moore et al., 1974; Johnson and Caldwell, 1974; Moser, 1974; Johnson and Tieszen, (in press). In addition, a number of laboratory gas exchange studies have been conducted with arctic and alpine tundra plants (Mooney and Billings, 1961; Mooney, 1963; Scott and Billings, 1964; Mooney and Johnson, 1965). Such studies have been reviewed by Larcher (1957), Tranquillini (1964), Billings and Mooney (1968), Bliss (1971), Billings (1974), and Tieszen and Wieland (in press).

The photosynthetic mechanism of tundra plants must cope with the characteristically low growing season temperatures and the short growing season of tundra environments. Although water stress is another important selective force in many environments, it is not commonly considered to be of particular importance in tundra environments. However, even though large portions of tundra have an abundance of water, many tundra sites can develop moderate to relatively severe atmospheric and soil moisture stress levels. Arctic tundra habitats such as low center polygons and polygon troughs typically have standing water during a large portion of the growing season. However, areas such as exposed high-center polygons and beach ridges can exhibit soil water potentials, Ψ_s, below -15 bars (Teeri, 1973). Bliss (1956) has noted similar microsite soil moisture variability in the Medicine Bow Mountains in Wyoming. Bliss (1956) found a wet alpine meadow site to be constantly saturated, whereas soil moisture potential in a fellfield site was often below -15 bars.

In addition to this soil moisture microsite variability, atmospheric moisture stress can be relatively severe in tundra environments. Salisbury and Spomer (1964) have measured leaf-to-air temperature gradients of more than 20°C in alpine tundra areas of Colorado. Though much less frequent, similar gradients may be reached in some arctic tundra sites. For example, Mayo, Despain, and Van Zinderen Bakker (1973) report that leaf temperatures for _Dryas integrifolia_ can frequently be 30°C above air temperature. With these large leaf-to-air temperature gradients, the water vapor difference between saturated leaf vapor pressure and ambient air vapor pressure, WVD, can exceed 20 mb in some instances. In contrast, when relative humidity is high and leaf temperature is close to air temperature, the WVD may be less than 1 mb. Thus, tundra environments may be expected to exhibit a large degree of microsite variability with respect to moisture stress. As a result, plant moisture stress may develop in many years in the more exposed sites and in very dry years may even occur in the more mesic tundra microsites.

Plant water stress may develop because of low soil moisture contents or temporarily strong environmental demands such as high insolation and large evaporative gradients. If the evaporative demands for transpiration are large, water absorption may lag behind transpiration (Slatyer, 1960; Gardner, 1964; Kramer, 1969). Using an Ohm's Law analog, this absorption lag may result from liquid phase water transfer resistances encountered from the soil to the root (soil resistance) and from the root to the leaf evaporative sites (plant resistance). The generalized equation of Van den Honert (1948) can be used as an acceptable approximation for this relationship and is expressed as follows:

$$R_s + R_p = \frac{\Psi_s - \Psi_1}{T} \quad (\mathrm{bar \cdot sec \cdot cm^{-1}}) \qquad (1)$$

where R_s and R_p are the resistances to water flow in the soil and the plant, respectively, Ψ_s is the soil water potential, Ψ_1 is the leaf water potential, and T is transpiration or water flux rate through the system.

The R_p term has been partitioned into components by Kramer (1969). He concludes that the largest component in R_p resides in the roots with the leaves comprising less and the least resistance contained in the stem where water movement takes place largely in the vascular conduction system. For example, results of Jensen, Taylor, and Wiebe (1961) suggest that the root resistance of sunflower is nearly twice as great as the leaf resistance and over three times as great as the stem resistance. However, recently Boyer (1974) has presented evidence that at very low transpiration rates much of the R_p resistance may reside in the leaves.

A number of studies suggest that appreciable R_s are exhibited in the soil even at Ψ_s above -1 bar (Gingrich and Russell, 1957; Peters, 1957; Denmead and Shaw, 1962; Gardner and Ehlig, 1962; Macklon and Weatherly, 1965; Etherington, 1967; Ehlig, Gardner, and Clark, 1968; Shinn and Lemon, 1968; Tinklin and Weatherley, 1968). However, Newman (1969b) has reviewed these studies and concluded that their results may be open to alternative explanations. Newman (1969a) concluded that R_s does not become appreciable until the soil is near or beyond the permanent wilting point. Indeed, calculations by Sykes and Loomis (1967), Lawlor (1972), and Hansen (1974a, 1974b) suggest that R_s is less than the R_p until soil moisture approaches the permanent wilting point.

If water absorption by the roots lags behind water loss through transpiration, leaf water stress may develop. In order to recover a favorable water balance plants can (Tranquillini, 1963):

1. intensify water absorption
    a) through extension of their root system by growth, thereby reaching parts of the soil which may still be moist
    b) through a decrease in tissue water potential by which they are able to intensify the water potential gradient from the soil to the plant.
2. reduce water loss
    a) through reduction of transpiring surfaces
    b) through increases in leaf diffusive resistances to water transfer.

When water loss through transpiration exceeds water absorption, concomitant declines in leaf water potential may be produced and may eventually result in stomatal closure. This stomatal closure is reflected in an increased stomatal diffusion resistance to water vapor flux which appears as r_s in the following Ohm's Law analog:

$$T = \frac{(VD)_{leaf} - (VD)_{air}}{(r_s + r_a)} \quad (mgH_2O \cdot dm^{-2} \cdot hr^{-1}) \qquad (2)$$

where T is transpirational water flux, VD_{leaf} is vapor density of the leaf assumed to be at saturation at the prevailing leaf temperature, VD_{air} is vapor density of the ambient air, and r_s and r_a are stomatal and boundary layer resistances to water vapor exchange, respectively.

This increased stomatal resistance not only restricts water loss, but also reduces photosynthesis. The water vapor leaf diffusive resistances as calculated above can be extrapolated to carbon dioxide leaf diffusive resistances using a multiplier (1.594) which relates the diffusion coefficients of carbon dioxide and water vapor (McPherson and Slatyer, 1973). Since photosynthesis is dependent upon not only leaf diffusive processes but also metabolic processes, an additional resistance must be incorporated into an Ohm's Law analogy for photosynthesis. The equation for photosynthesis can be expressed according to the following equation developed by Gaastra (1959):

$$P = \frac{(CO_2)_e - (CO_2)_i}{(r'_a + r'_s) + r'_m} \quad (mgCO_2 \cdot dm^{-2} \cdot hr^{-1}) \qquad (3)$$

where P is net photosynthesis, $(CO_2)_e$ is the carbon dioxide concentration outside the leaf, $(CO_2)_i$ is the carbon dioxide concentration at the carboxylation site which is necessarily assumed to be zero, $(r'_a + r'_s)$ and r'_m are the leaf diffusive and mesophyll resistance to carbon dioxide exchange, respectively. The mesophyll resistance term originally developed by Gaastra (1959) is referred to in this study as residual resistance. Although Gaastra (1959) originally developed this resistance term to refer mainly to intracellular CO_2 diffusion resistance, subsequently this resistance has been viewed to include both diffusive and metabolic components (Jones and Slatyer, 1972), and thus more appropriately is termed as the residual resistance, r'_r (Gifford and Musgrave, 1972).

Reductions in photosynthesis with increasing water stress are well established and can occur in some mesophytes at Ψ_1 as high as -1 to -3 bars (Schneider and Childers, 1941; Loustalot, 1945; Bordeau, 1954; Brix, 1962). However, the photosynthetic reduction threshold Ψ_1 for a number of other mesophytes seems to range between

-7 to -16 bars (Kanemasu and Tanner, 1969; Boyer, 1970; Duniway, 1971; Jordan and Ritchie, 1971). These photosynthetic reductions may be the result of three major factors (Slavik, 1965; Slatyer, 1967; Crafts, 1968; DePuit (in press): 1) hydroactive stomatal closure, bringing about a reduced CO_2 supply to the mesophyll (affecting r'_s), 2) water stress effects on the biochemical processes involved in photosynthesis (reflected in r'_r), and 3) water stress effects on the processes of respiration in the light (also reflected in r'_r).

Increasing r'_s has been shown to be the major cause of reduced photosynthesis in many water-stressed crop species (e.g., Troughton, 1969; Boyer, 1970; Stevenson and Shaw, 1971; Teare and Kanemasu, 1972; Moldau, 1973). However, there is additional evidence which suggests that increased r'_r may also be important in explaining a substantial degree of the photosynthetic depression (e.g., Gale, Kohl, and Hagan, 1966; Hellmuth, 1969; Boyer and Bowen, 1970; Redshaw and Meidner, 1972; Beadle et al., 1973; DePuit and Caldwell, 1975).

As stated earlier, these increases in r'_r may at least in part reflect water stress effects on the biochemical processes involved in photosynthesis. For example, Parker (1972) suggests that water stress may alter membrane integrity, disrupt chloroplast structure, or impair enzyme function. In addition, increases in r'_r may be reflecting increases in respiration in the light concomitant with photosynthesis (Levitt, 1972), and may reflect either increased mitochondrial respiration or photorespiration. Although normal mitochondrial respiration as assayed in the dark may be somewhat depressed when the plant is in the light (Jackson and Volk, 1970), at least part of the respiratory CO_2 losses from leaves in the light may be indicated by dark respiration rates. Although dark respiration rates of some species seem to exhibit general declines with increasing water stress (e.g., Greenway and Hiller, 1967; Boyer, 1971), increased dark respiration rates following initial declines have been noted for some arid and Mediterranean species (e.g., Mooney, 1969; DePuit and Caldwell, 1975). However, as Ludwig and Canvin (1971b)suggest, there remains the possibility that photorespiration may increase when water stress intensifies.

Cleland (1967) and Hsiao (1973) have noted that other physiological processes such as cell expansion may be inhibited at much lower water stress levels than photosynthesis. In fact results of Boyer (1968) suggest that leaf enlargement is so sensitive to water stress that it may be largely restricted to night periods. The importance of turgor pressure in supplying the necessary force for cell expansion has long been considered crucial (Vaadia, Raney, and Hagan, 1961; Lockhart, 1965; Cleland, 1971). For example, results of Wadleigh and Gauch (1948) showed a progressive decline in the rate of cotton leaf elongation with increasing soil moisture stress until elongation ceased at near zero turgor pressure. Similarly, Plaut and Ordin (1961) showed a very close agreement between turgor pressure and leaf enlargement in sunflower and almond. More recently Acevedo, Hsiao, and Henderson (1971) reported that rewatering mildly stressed corn plants permitted rapid resumption of leaf elongation. This effect of turgor pressure on cell enlargement would necessarily have an indirect effect on plant productivity since reduced cell size would ultimately result in reduced photosynthetic leaf area. As a result, even though water stress may not be severe enough to limit primary production through declines in photosynthetic rates in tundra species, reduction of productivity through depressed growth rates may occur more frequently.

Since moisture stress affects a number of important physiological processes in plants and since significant moisture stresses may develop in at least some tundra areas, this study was initiated to determine whether plant physiological behavior to water stress may be one important contributing factor in determining the microsite distributions of tundra plants. However, it should be emphasized that even though effects of water stress on physiological processes may be important in themselves, these should always be applied in conjunction with the other multivariate biotic and abiotic factors which constitute the environmental complex of the plant.

CHAPTER II

DESIGN DESCRIPTION

Objectives and Hypotheses

The first objective of this study was to determine to what degree moisture stress develops in alpine tundra plants under field conditions. Therefore, a field study was designed to assess the degree of plant moisture stress which may develop in representative sites in the alpine tundra in Colorado. These experiments were designed to test the hypothesis that significant plant moisture stress may develop in at least the more exposed alpine tundra areas.

If significant plant moisture stresses develop in the alpine tundra and if physiological adaptations to water stress are important determining factors in the distribution of alpine tundra species, plant moisture stress may be expected to have a larger inhibitory effect upon the photosynthetic capacities of species restricted to wet sites as compared with species having a broader distribution. To address this hypothesis additional field studies were designed to investigate the effect of plant moisture stress on the photosynthetic capacity of two alpine tundra species with different microsite distributions. The species examined in this field study were *Deschampsia caespitosa* (L.) Beauv. which is typically found in wet meadow habitats and *Geum rossii* (R.Br.) Ser., a species which ranges from wet meadow to exposed fellfield habitats.

A second objective of this study was to determine how atmospheric and soil moisture stress each impact on the gas exchange of tundra species with different local distributions. The same alpine tundra species as used for the field study, Geum rossii and Deschampsia caespitosa, were used in this laboratory study. In addition, to determine if the generalizations made for alpine tundra species could be extrapolated to plant species from a geographically different location, two arctic tundra species with local distributions similar to their alpine counterparts were selected for study. The arctic tundra species investigated were Dupontia fischeri R. Br. which is restricted mainly to wet meadow areas and Carex aquatilis Wahlenb., a species covering a wider range of habitat types from wet meadows to drier, more exposed areas.

Laboratory experiments enabled precise measurements of net photosynthesis, transpiration, and dark respiration as affected by the independent effects of atmospheric and soil moisture stress. This information allowed partitioning of the gas exchange resistances and enabled assessment of the water use efficiency for photosynthesis of these tundra species. These laboratory experiments were designed to test the hypothesis that increasing atmospheric and soil moisture stress result in decreased photosynthetic capacities to a greater extent in species restricted to wet areas than in species with a broader microsite distribution. In addition, it was hypothesized that these photosynthetic reductions would be due to not only reduced stomatal aperture, reflected in increased stomatal diffusion resistance, but also to greater non-stomatal or residual resistance, indicating a direct impact of water stress on the photosynthetic apparatus.

The third objective of this study was to determine other attributes which may be important in determining the distributions of these tundra species. For example, one such attribute may be the liquid phase water transfer resistance from the soil to the leaf. By exposing these tundra plants to a range of soil moisture regimes, it was possible to address the hypothesis that the wider ranging species were able to maintain a lower water transfer resistance over a wider range of soil moisture stress conditions than species restricted to more mesic areas.

Since leaf enlargement is closely associated with turgor pressure, another important attribute may be the ability to minimize reductions in leaf turgor pressure as moisture stress increases. Therefore, a laboratory study was designed to determine the reduction of turgor pressure over a range of plant moisture regimes. Such experiments were conducted to test the hypothesis that tundra species having a wider ranging local distribution are better able to maintain turgor over a broader range of moisture stress conditions than species restricted mainly to wet tundra areas.

Site Descriptions

The study site where the alpine tundra field study was conducted and where the alpine plant material was obtained for the laboratory study is located on a gently sloping saddle area on Niwot Ridge (40° 04'N, 105° 36'W, 3476 m elev.) in the Front Range of the

Colorado Rocky Mountains. The site has a southwest aspect, a 2° slope, and is near the U. S. International Biological Programme (IBP) Tundra Biome intensive study sites. The vegetation of the area is characterized by low perennial grasses, sedges, and herbs. The specific site where this study was conducted is dominated by Deschampsia caespitosa, Geum rossii, and Trifolium parryi Gray. The flora of the area has been described by Harrington (1954) and by Weber (1967).

During the 1972 field season, the two IBP Tundra Biome intensive sites were also sampled periodically throughout the growing season for dawn and midday leaf water potentials of Geum rossii and Deschampsia caespitosa. A thorough characterization of these IBP intensive sites is contained in Fareed and Caldwell (1975). One of these sites is a Kobresia meadow community dominated by Kobresia myosuroides (Vill.) Fiori and Pool. with subdominants of Geum rossii and Carex rupestris All. This site has a southwest aspect, a 5° slope, and is typical of a well-developed, mesic meadow which may be snow-free for up to 250 days per year. The second site is a Deschampsia meadow community dominated by Deschampsia caespitosa, Artemisia scopulorum Gray, and Geum rossii. This Deschampsia site has a southeast aspect, a 4° slope, and is exposed to heavy snow melt water which may persist until late June.

The geology of this area has been discussed by Marr (1967), Benedict (1967), and Mahney (1970). Bedrock in this area generally consists of Precambrian granites to granodiorites and metamorphics in large batholithic masses. In addition Tertiary-age quartz monzonites to diorites occur as stocks, dikes, and sills injected into the Precambrián rocks. Retzer (1956) has described the soils in the Colorado Rocky Mountains and states that these soils have typically undergone geomorphic processes associated with heaving, thrusting, sorting, and down-slope movement. Furthermore, Marr (1967) states that the soils on Niwot Ridge are coarse to silty loams and range to 60 cm in depth. Meadow soils are quite well-developed and have upper horizons rich in humus, whereas fellfield areas have minimum soil horizon differentiation and can be less than 2 cm in depth.

Original plant cultures of arctic tundra plant species used in the laboratory portion of this study were acquired from Barrow, Alaska (71° 20'N, 156° 46'W, 3 m elev.), near the U. S. IBP Tundra Biome study sites which are dominated by low perennial grasses, sedges, and herbs. This study site is composed primarily of Eriophorum angustifolium Honck., Dupontia fischeri, and Carex aquatilis. Studies of the canopy characterization and the seasonal course of aboveground production of this site have been conducted by Caldwell, Tieszen, and Fareed (1974) and Tieszen (1972). Additional floristic composition and vegetation information of the area is contained in Britton (1957), Clebsch and Shanks (1968), Hultén (1968), and Dennis and Johnson (1970).

Brown (1970) reviews the general environmental setting of the Barrow area and states that this area is an emergent coastal plain underlain by perennially frozen ground which may exceed a depth of 300 meters. The physical aspect of this area is dominated by polygonal ground, oriented lakes, and rapidly eroding shorelines, all of which are reflections of perennially frozen ground. According to Drew (1957), the coastal plain soils are composed of silts, fine sands, and gravels of the Pleistocene age which overlie rocks of the Cretaceous and Tertiary age. Even though a large portion of these soils are predominantly wet with an average seasonal thaw of approximately 40 cm, there are raised beach ridges and high center polygons which are well-drained and may undergo seasonal thaw in excess of 100 cm.

Laboratory Plant Material

Sod blocks from near the Niwot Ridge alpine tundra IBP intensive site were removed in late August and were placed in a freezer. As alpine plant material was needed, these sod blocks were placed in flats in the greenhouse. Arctic tundra plant specimens were obtained from stock plant cultures maintained at Augustana College, Sioux Falls, South Dakota. Original cultures of these arctic tundra species were acquired from near the arctic tundra IBP intensive site near Barrow, Alaska.

Arctic and alpine plant material from each of the sites was transplanted into plastic pots (13 cm diameter, 13 cm height) using a soil mixture consisting of 2 parts peat moss, 2 parts loam, and 1 part vermiculite. These potted plants were grown in a greenhouse with day temperatures reaching 21°C and 10°C at night with relative humidities ranging between 45-65 percent. Ambient radiation was used during the spring and summer with supplementary fluorescent lighting supplied during fall and winter.

The relationships of photosynthesis to light and temperature were established to determine how closely the response of these plants grown under these conditions corresponded to those of field plants. Light saturation for the arctic species, <u>Carex</u> and <u>Dupontia</u> (Figure 1), was near 800 μeinsteins$\cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) and near 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ for <u>Geum</u> and <u>Deschampsia</u>, the alpine species (Figure 2). Temperature optima for <u>Carex</u> and <u>Dupontia</u> were near 15°C (Figure 3), while <u>Geum</u> and <u>Deschampsia</u> exhibited optima at 20°C and 25°C, respectively (Figure 4). These results agree closely with the response of these species under field conditions (Tieszen, 1973; Moore et al., 1974).

The higher light saturation of photosynthesis observed in the alpine species than in the arctic species has been well established by others (Cartellieri, 1940; Clebsch, 1960; Mooney and Billings, 1961). Björkman and Holmgren (1963) suggest that these light saturation values reflect the lower light intensities under which arctic plant evolution has occurred. Similarly, temperature optima for arctic plant species generally tend to be 5 to 10°C below their alpine counterparts (Clebsch, 1960; Mooney and Billings, 1961; Mooney and Johnson, 1965).

Figure 1. Net photosynthesis and transpiration rates of Dupontia fischeri and Carex aquatilis as a function of light intensity at a leaf temperature of 20°C and a WVD of 10 mb. Each point represents the mean of two replicates with the vertical bars representing ± one standard deviation.

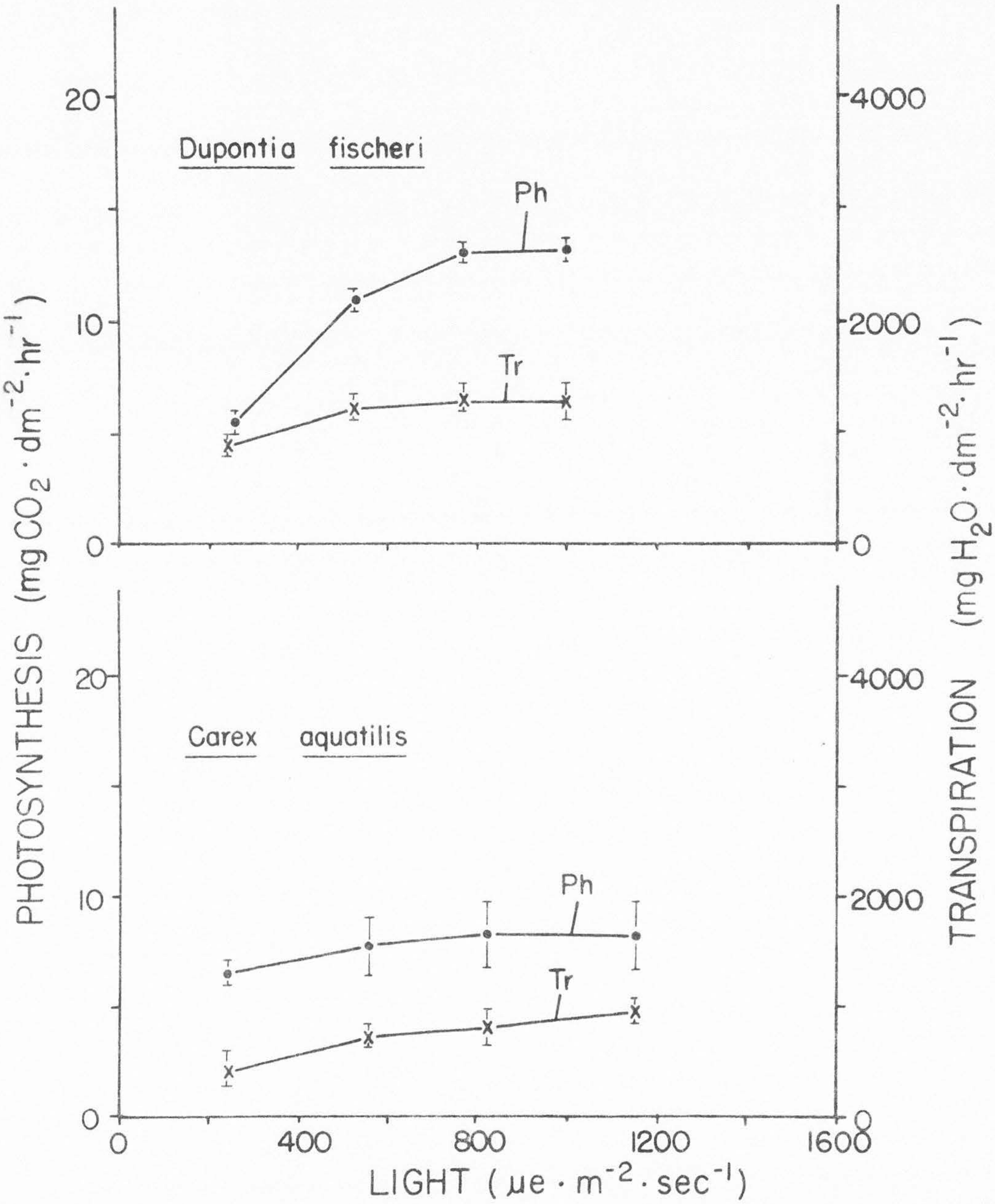

Dupontia fischeri
Ph
Tr
Carex aquatilis
Ph
Tr
20
10
0
4000
2000
0
0
400
800
1200
1600
PHOTOSYNTHESIS (mg CO$_2$ · dm^{-2} · hr^{-1})
TRANSPIRATION (mg H$_2$O · dm^{-2} · hr^{-1})
LIGHT (μe · m^{-2} · sec^{-1})

Figure 2. Net photosynthesis and transpiration rates of Deschampsia caespitosa and Geum rossii as a function of light intensity at a leaf temperature of 20°C and a WVD of 10 mb. Each point represents the mean of two replicates with the vertical bars representing ± one standard deviation.

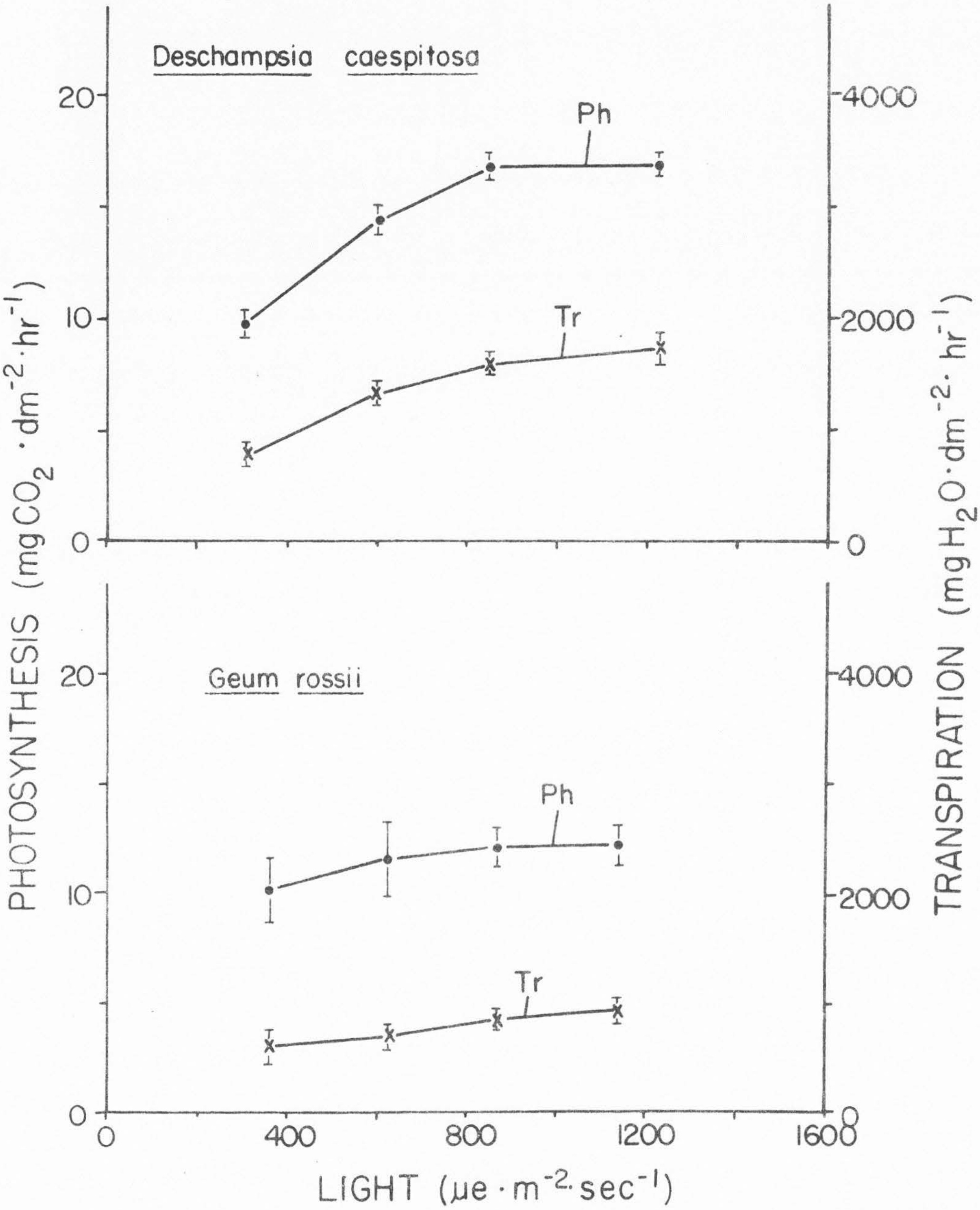

Deschampsia caespitosa
Ph
Tr
Geum rossii
Ph
Tr
PHOTOSYNTHESIS (mg CO$_2$ · dm^{-2} · hr^{-1})
TRANSPIRATION (mg H$_2$O · dm^{-2} · hr^{-1})
0
10
20
0
2000
4000
0
400
800
1200
1600
LIGHT (μe · m^{-2} · sec^{-1})

Figure 3. Net photosynthesis and transpiration rates of _Dupontia fischeri_ and _Carex aquatilis_ as a function of leaf temperature at 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point represents the mean of four replicates with the vertical bars representing ± one standard deviation.

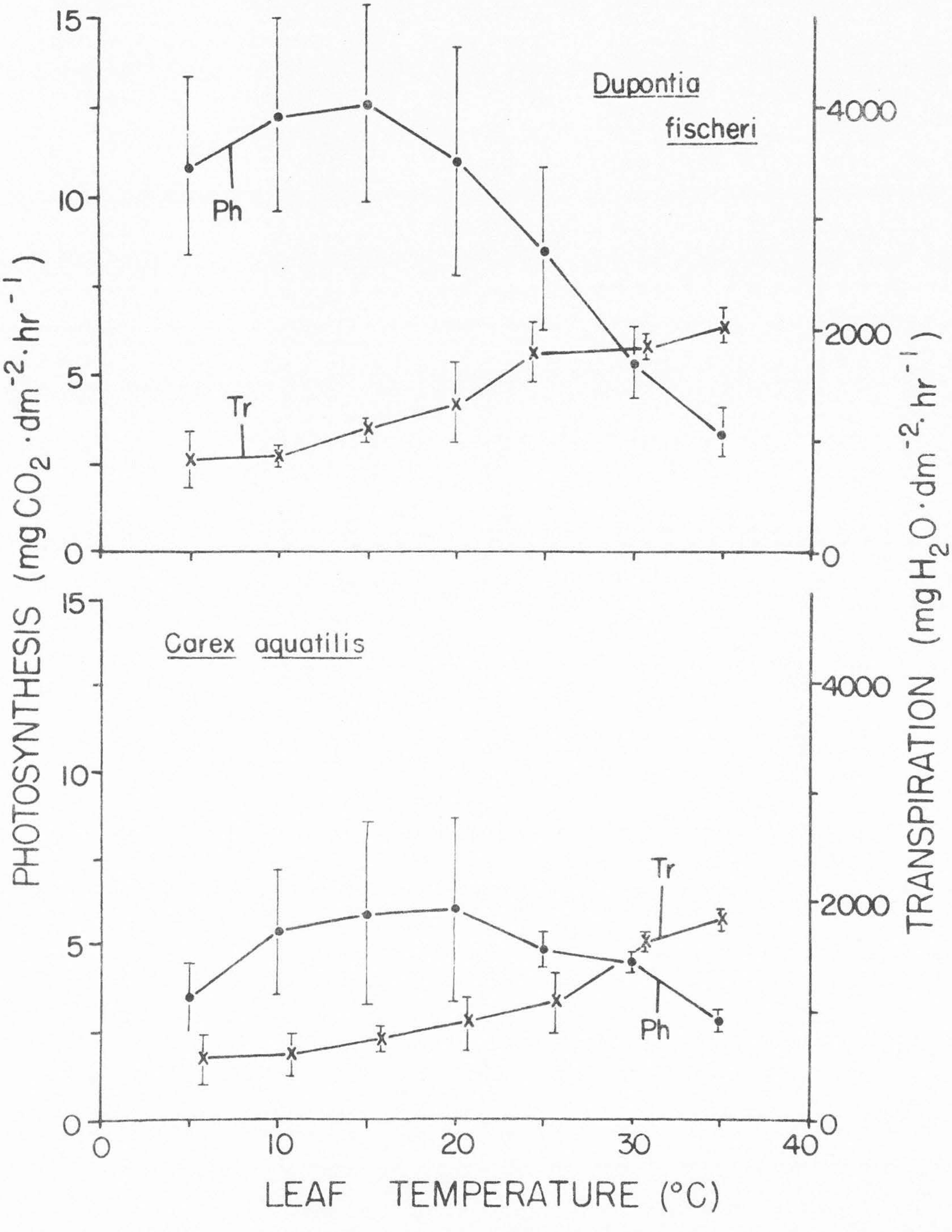
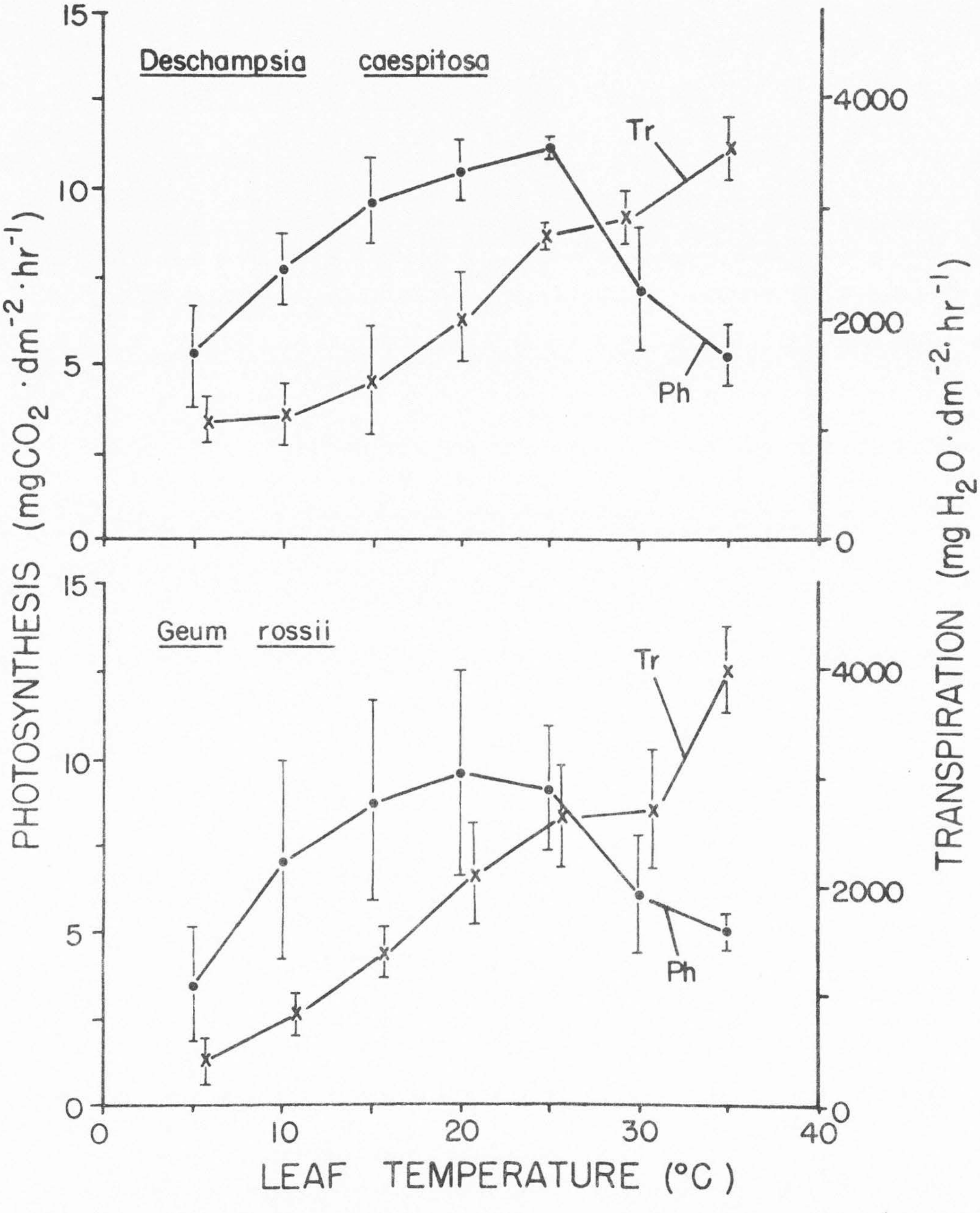

15
10
5
0
Dupontia
fischeri
Ph
Tr
4000
2000
0
15
Carex aquatilis
10
5
0
Tr
Ph
4000
2000
0
0
10
20
30
40
PHOTOSYNTHESIS (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
TRANSPIRATION (mg $H_2O \cdot dm^{-2} \cdot hr^{-1}$)
LEAF TEMPERATURE (°C)

Figure 4. Net photosynthesis and transpiration rates of *Deschampsia caespitosa* and *Geum rossii* as a function of leaf temperature at 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point represents the mean of four replicates with the vertical bars representing ± one standard deviation.


Deschampsia caespitosa
Geum rossii
Tr
Ph
15
10
5
0
4000
2000
0
PHOTOSYNTHESIS (mgCO$_2$ · dm^{-2} · hr^{-1})
TRANSPIRATION (mg H$_2$O · dm^{-2} · hr^{-1})
0
10
20
30
40
LEAF TEMPERATURE (°C)

CHAPTER III

FIELD STUDY

Introduction

Plant survival and productivity in the harsh tundra environment hinge critically on the photosynthetic capacity of these plants. Although the time of snowmelt at a particular site is of decisive importance in terms of initiation of growth and photosynthesis at the beginning of the growing season, photosynthetic capacity of these tundra plants is likely controlled by other factors during the later phases of the growing season. One factor of importance may be water stress.

Johnson, Caldwell and Tieszen (1974) reported field measurements of the photosynthetic capacity for leaves of the same age over a limited plant moisture stress range in selected alpine tundra species. Although linear regressions of these results for *Geum rossii* and *Deschampsia caespitosa* indicated a weak relationship between plant moisture stress and photosynthesis, these measurements were taken over a limited plant moisture stress range.

This present field study was initiated to yield information on the degree of plant moisture stress which may develop in a number of selected sites in the alpine tundra on Niwot Ridge in Colorado, and also to obtain data on the effects of a wider range of plant moisture stress on the photosynthetic capacities of *Geum rossii* and *Deschampsia caespitosa*.

Methods

The two IBP Tundra Biome intensive alpine tundra study sites were sampled periodically thoughout the 1972 field season for dawn and midday leaf water potentials of *Geum rossii* and *Deschampsia caespitosa*. Leaf water potentials were measured using the Scholander pressure chamber technique (Waring and Cleary, 1967). Four replicates were taken for each species.

During the 1973 field season, irrigated and non-irrigated plots containing both *Geum rossii* and *Deschampsia caespitosa* were established at the beginning of the field season near the IBP Tundra Biome intensive sites on Niwot Ridge in Colorado. The irrigated plots were watered every two days with approximately 20 ℓ of water obtained from snow meltwater of a nearby persisting snowfield. In addition the irrigated plots were wetted immediately before photosynthetic determinations on plants within these plots were made. These plots allowed for varying plant water status throughout the growing season and thus allowed a wider range of plant moisture than normally encountered in this particular site.

Leaf photosynthetic measurements were determined using a portable $^{14}CO_2$ field system. The field system and procedure have been described by Tiezsen, Johnson, and Caldwell (1974). The field system consists of a plexiglass leaf chamber which is temperature controlled by a Peltier thermoelectric stage. The procedure involves exposing an intact leaf to a $^{14}CO_2$ air mixture, immediately cooling the leaf sample in the field following exposure, subsequent drying of the exposed leaf sample, combusting this sample, and radioactivity counting using liquid scintillation techniques.

According to studies by Ludwig and Canvin (1971a), net $^{14}CO_2$ uptake in a leaf is maximum at exposure periods less than 30 sec. This initial period approximates gross CO_2 influx. After 30 sec, net CO_2 uptake decreases as the exposure time in $^{14}CO_2$ is extended and after 10 min approaches normal net CO_2 exchange rates. This decrease in $^{14}CO_2$ uptake is associated with $^{14}CO_2$ evolution from the leaf. Thus, with exposure times of 1 min used in this study, CO_2 uptake measured was closer to gross CO_2 uptake than net photosynthesis.

All CO_2 uptake determinations were conducted under a constant chamber temperature of 10±0.5°C which is representative of the mean daytime growing season temperatures at the study site. Chamber temperatures were measured using a shielded copper-constantan fine-wire thermocouple. Leaf temperatures were also monitored and were always within ±1°C of chamber air temperature. Artificial irradiation was provided by a high intensity incandescent lamp (100 W) and was monitored with a Lambda Co. Model LI-190SR quantum sensor. A constant intensity of 2,700 ± 200 $\mu e \cdot m^{-2} \cdot sec^{-1}$ in the 400 to 700 nm wavelength range was used for all determinations and is approximately equal to maximum midday solar radiation. In addition, the air stream was bubbled through water which yielded a high relative humidity within the plexiglass leaf chamber. A period of 5 min was allowed for the leaf to attain a steady state gas exchange rate under these environmental conditions before $^{14}CO_2$ exposure.

Immediately following $^{14}CO_2$ exposure, the leaf water potential, Ψ_1, was determined using the Scholander pressure chamber technique (Waring and Cleary, 1967). Since the water relations (Levitt, 1972) and the photosynthetic capacities (Johnson and Caldwell, 1974) of leaves can change with age and stage of development, only leaves which were the longest, most recently fully expanded on the plant were used during these field experiments.

Leaf lengths and widths for _Deschampsia caespitosa_ were measured to the nearest 0.5 mm and could lead to a ±0.3 mm^2 error in area measurements. Although length and width measurements for _Geum rossii_ were also measured to the nearest 0.5 mm, as many as four leaflets were measured and as a result errors in area measurement could be as high as ±1.0 mm^2. When compared to the smallest areas measured in each of these species, these area determinations would represent an accuracy of ±5 percent for _Deschampsia_ and ±12 percent for _Geum_.

The seasonal trend of soil water potential, Ψ_s, for _Geum_ and _Deschampsia_ in the non-irrigated plots was determined throughout the 1973 field season. Soil samples from -10 and -20 cm depths were obtained using a 2.5 cm diameter aluminum corer. These soil samples were placed into a sample holder and sealed in the air-tight teflon chamber of a Wescor C-51 psychrometer assembly. A 10 min equilibration period was allowed before a Peltier cooling period and subsequent microvolt outputs were determined. These outputs were converted to soil water potential values from calibrations made against saturated NaCl solutions of known molality. Three replicates were taken from each of the two soil depths.

Results and Discussion

The seasonal trend of soil water potential, Ψ_s, in the non-irrigated plots for both Geum and Deschampsia showed very little fluctuation throughout the 1973 field season (Figure 5). The -10 cm Ψ_s was used for Deschampsia, while the -20 cm Ψ_s was used for Geum and correspond approximately to the area of maximum rooting densities for these species. These field measurements of Ψ_s taken during the summer of 1973, a summer of below-average precipitation (e.g. mean summer precipitation is 19 cm and summer of 1973 was 13 cm), indicate that Ψ_s values in the non-irrigated plots on Niwot Ridge were never observed below -5 bars. The Ψ_s for Deschampsia was consistently above -5 bars, while Ψ_s for Geum did not achieve values less than -2 bars. Additional Ψ_s determinations from an exposed fellfield area on Niwot Ridge indicated that Ψ_s reached a value as low as -15 bars. The seasonal trend of Ψ_l (Figure 5) indicated that the most negative Ψ_l occurred at the beginning and the end of the field season with Ψ_l as low as -25 bars for Deschampsia and -17 bars for Geum.

Dawn and midday Ψ_l for Geum and Deschampsia were determined in the Kobresia and Deschampsia IBP intensive study sites during the 1972 field season (Figures 6 and 7). Dawn and midday Ψ_l values decreased throughout the season for both Geum and Deschampsia and were consistently more negative in the Kobresia site as compared to the Deschampsia site. A Ψ_l of -31 bars was the most negative Ψ_l exhibited by Deschampsia and occurred in the Kobresia site near

Figure 5. Seasonal trends of Ψ_l and Ψ_s for *Deschampsia caespitosa* and *Geum rossii*. Each Ψ_l is the mean of four to eight replicates with the vertical bars representing ± one standard error. Ψ_s was determined at -10 cm for *Deschampsia* and -20 cm for *Geum* which correspond approximately to the area of maximum rooting densities, respectively, and correspond to the mean of three replicates. All measurements were determined at 0800 solar time.

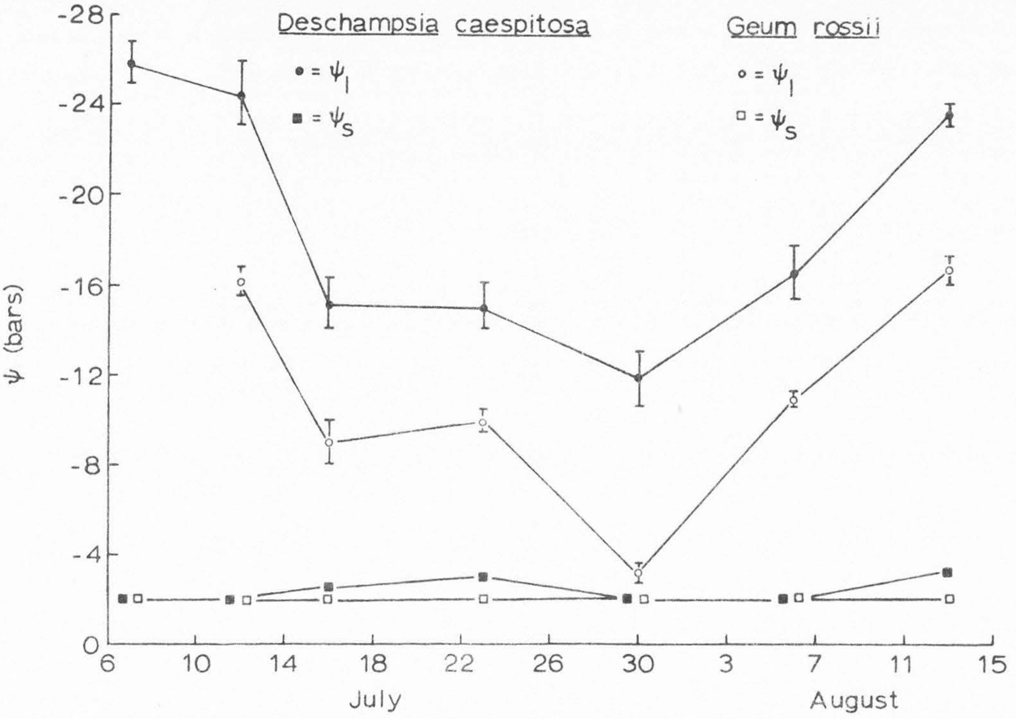

Deschampsia caespitosa
● = ψ_l
■ = ψ_s
Geum rossii
○ = ψ_l
□ = ψ_s
ψ (bars)
-28
-24
-20
-16
-12
-8
-4
0
6
10
14
18
22
26
30
3
7
11
15
July
August

Figure 6. Seasonal course of dawn (0530-0730 solar time) and midday (1100-1400 solar time) Ψ_1 of *Deschampsia caespitosa* in the *Kobresia* and *Deschampsia* IBP intensive sites on Niwot Ridge in Colorado. Each point represents mean of four replicates.

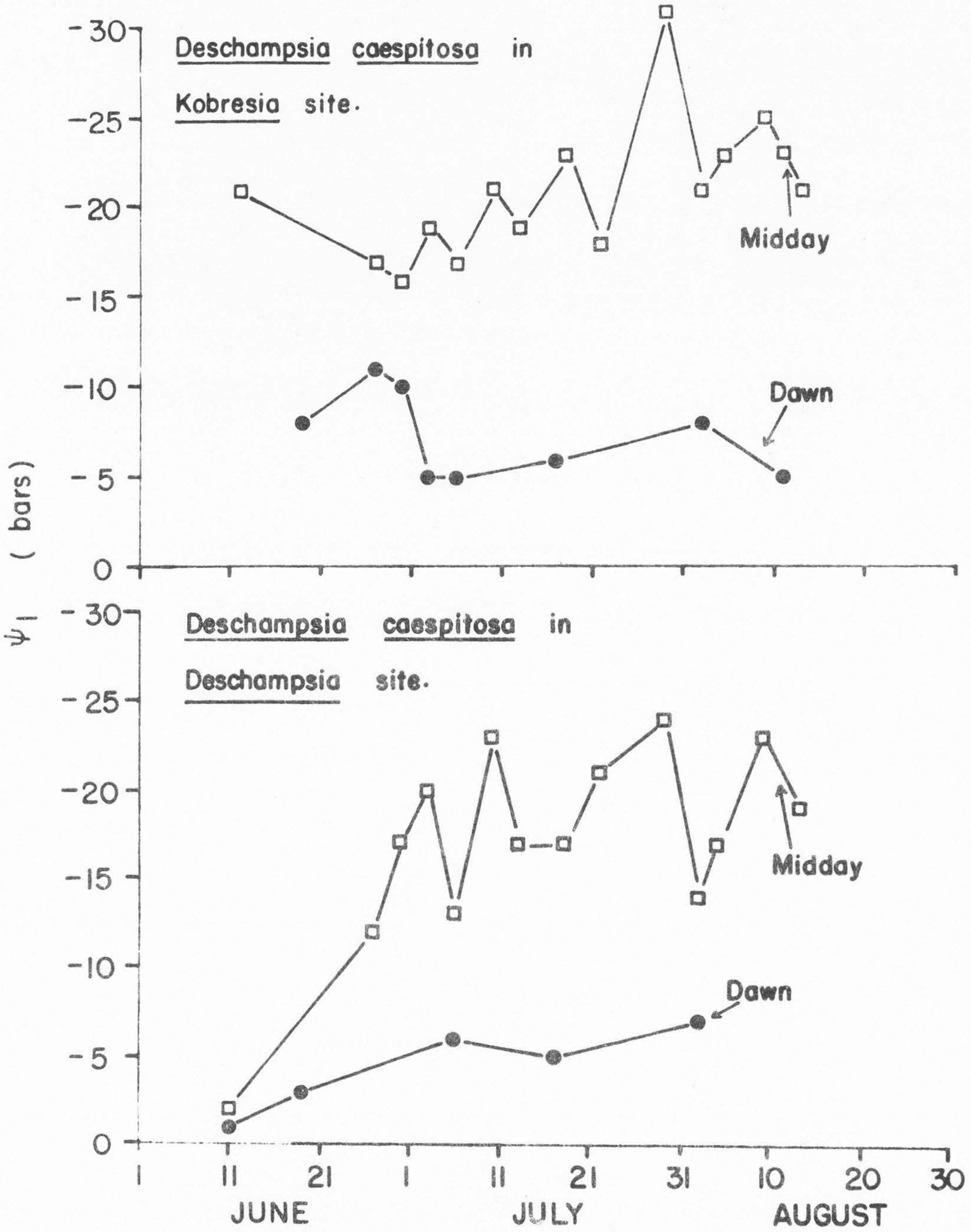
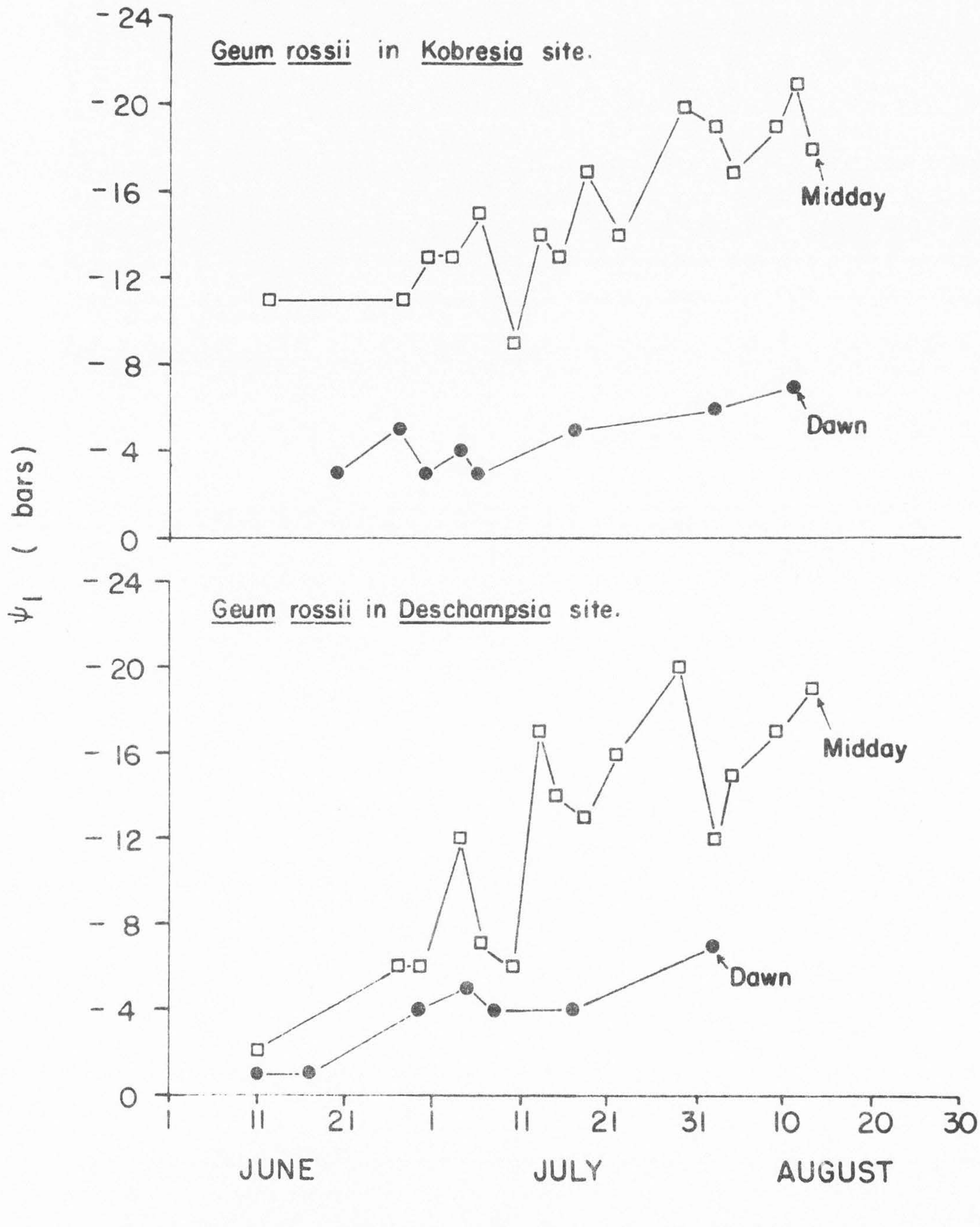

Deschampsia caespitosa in Kobresia site.
Midday
Dawn
Deschampsia caespitosa in Deschampsia site.
Midday
Dawn
ψl (bars)
-30
-25
-20
-15
-10
-5
0
1
11
21
1
11
21
31
10
20
30
JUNE
JULY
AUGUST

Figure 7. Seasonal course of dawn (0530-0730 solar time) and midday (1100-1400 solar time) Ψ_1 of *Geum rossii* in the *Kobresia* and *Deschampsia* IBP intensive sites on Niwot Ridge in Colorado. Each point represents the mean of four replicates.

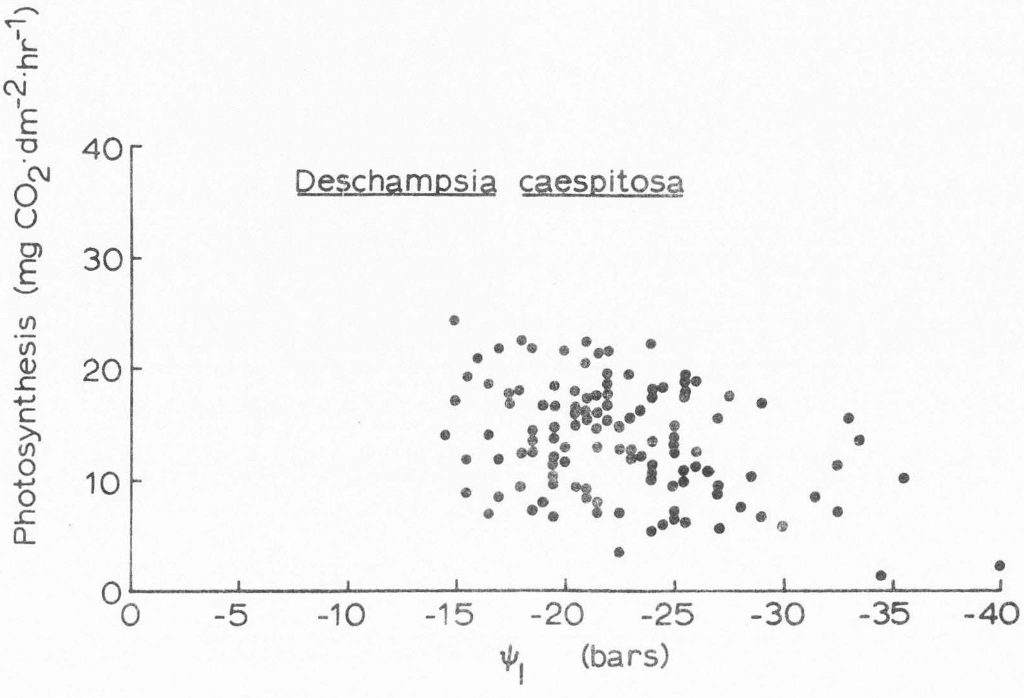

Geum rossii in Kobresia site.
Geum rossii in Deschampsia site.
Midday
Dawn
Midday
Dawn
ψ_l (bars)
- 24
- 20
- 16
- 12
- 8
- 4
0
1
11
21
1
11
21
31
10
20
30
JUNE
JULY
AUGUST

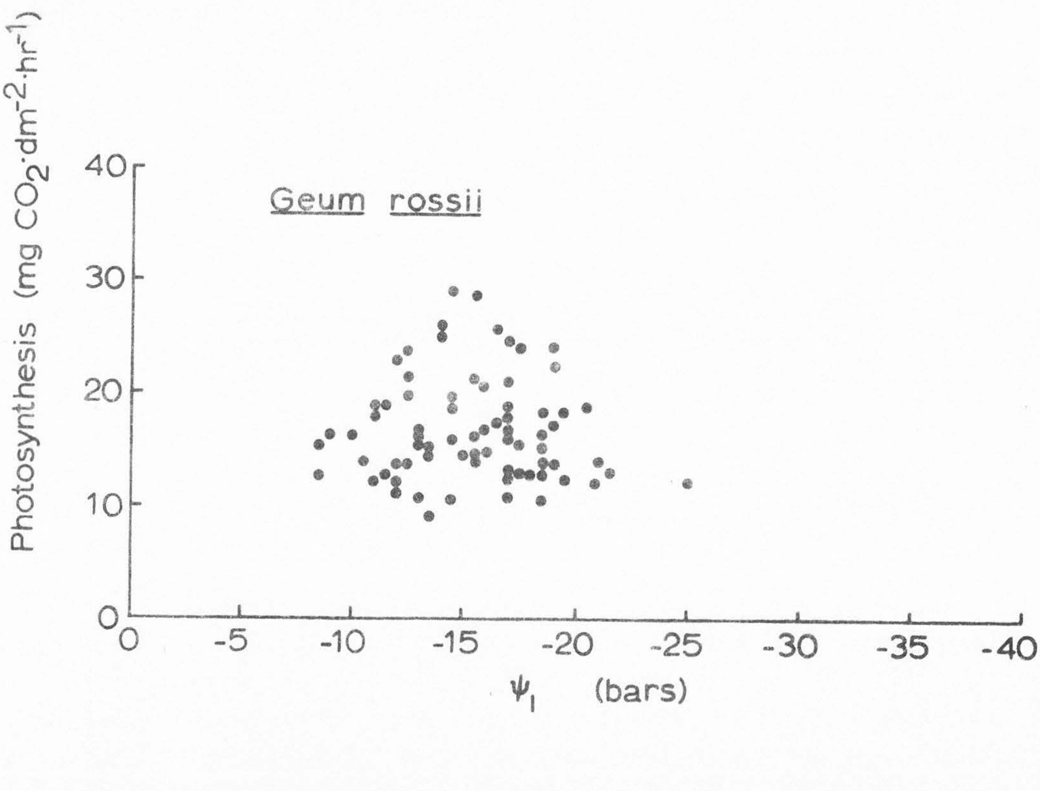
the end of July. The most negative Ψ_1, -21 bars, for Geum also occurred in the Kobresia site but was observed in the first part of August.

The effects of plant water stress upon leaf photosynthetic capacity for Geum and Deschampsia are presented in Figure 8. Both Geum and Deschampia show a high degree of variability with respect to photosynthesis at different Ψ_1. In Geum there was no apparent trend in this relationship, whereas a general trend of decreasing photosynthesis with increasing levels of plant water stress seemed to be suggested for Deschampsia.

Direct correlations between plant water potential and net photosynthesis have been found in desert shrub species (DePuit and Caldwell, 1973; Odening, Strain, and Oechel, 1974) and in soybean and sorghum leaves (Teare and Kanemasu, 1972). However, Hodges (1967) working with coniferous species and Dunn (1970) working with evergreen sclerophylls found somewhat elevated plant water potentials concurrent with water stress-induced stomatal closure and net photosynthesis reduction. DePuit (in press) has reviewed the literature on this aspect of photosynthesis and states that the best correlations between depressed net photosynthesis and lowered water potential have been obtained when soil or substrate water potentials are used (e.g., Bamberg et al., 1974; Morrow and Mooney, 1974; Reid, 1974). Therefore, Campbell and Harris (1974) suggest that soil rather than plant water potential may be the best correlative parameter in relating net photosynthesis to water potential.

Figure 8. Leaf photosynthetic rates at different Ψ_l for *Deschampsia caespitosa* and *Geum rossii* determined at a leaf temperature of 10°C, 2700 $\mu\text{e}\cdot\text{m}^{-2}\cdot\text{sec}^{-1}$ (400-700 nm) where photosynthesis was light-saturated, and a high relative humidity. All measurements were taken between 0700 and 1300 solar time during the field season between July 9 and August 14.


Deschampsia caespitosa
Photosynthesis (mg CO2·dm-2·hr-1)
40
30
20
10
0
0
-5
-10
-15
-20
-25
-30
-35
-40
ψl (bars)


Geum rossii
Photosynthesis (mg CO2·dm-2·hr-1)
40
30
20
10
0
0
-5
-10
-15
-20
-25
-30
-35
-40
ψl (bars)

Crafts (1968) suggested that plant water stress develops in flowering ornamentals and vegetable crops when Ψ_1 range between 0 and -5 bars, in field and crop plants down to -16 bars, and in desert plants from -20 to -80 bars. Thus, it seems that moisture stress may develop in many years in the more exposed sites and in very dry years may even occur in the more mesic tundra microsites. These results suggest that water stress may in at least some areas be a significant factor limiting primary productivity in the alpine tundra.

Even if future research fails to indicate that water potentials which directly limit photosynthetic capacity are widespread in alpine areas, the importance of water stress in altering phenological progression, leaf enlargement phenomena, the development of leaf senescence must still be considered as possible indirect effects on community primary production. For example, Newman (1965) reported that water stress hastened rosette senescence and, thus, reduced fruit and seed set in _Teesdalia nudicaulis_. In addition, Gates (1957) found that relative leaf growth rates in young tomato leaves were affected more than old leaves when water stress was imposed. Thus, leaves at various developmental stages within a plant responded differently to imposed water stress. This may be an extremely crucial factor in alpine tundra plants where the ontogenetic timing is geared with the surge and decline of individual photosynthetic activity so that one to several leaves operating near maximum photosynthetic capacity are always maintained during the growing season for any given plant (Johnson and Caldwell, 1974). Although leaves at the state of full expansion and prior to senescence may be only slightly influenced by water stress, any indirect effects on the ontogenetic timing of leaf development or an alternative deployment of carbon resources to other plant parts such as reproductive organs could be of considerable importance.

CHAPTER IV

LABORATORY GAS EXCHANGE STUDY

Introduction

As shown earlier in Chapter I, tundra environments exhibit a large degree of microsite variability with respect to moisture stress. As a result, plant moisture stress may develop in many years in the more exposed tundra microsites and in very dry years may even occur in the more mesic tundra microsites. If physiological adaptations of tundra plants to water stress are important determining factors in the distribution of these species, atmospheric and soil moisture stress may be expected to have a larger inhibitory effect upon the photosynthetic capacities of species restricted to wet sites as compared with species having a wider distribution. Klikoff (1965) suggested that such differences exist for timberline meadow species in the California Sierra Nevada.

Field measurements of the photosynthetic capacities of two alpine tundra species, *Geum rossii* and *Deschampsia caespitosa*, contained in Chapter III, did not indicate a strong dependency of photosynthetic capacity on moisture stress. These measurements were, however, taken over a rather limited range of plant moisture stress. This present study was initiated to determine possible differences in gas exchange behavior of tundra species which are typically restricted to wet site areas and those which have a wider distribution when these plants are exposed to a range of controlled atmospheric and soil moisture stress.

Methods

Deschampsia caespitosa and *Geum rossii* were the alpine tundra species investigated, while *Dupontia fischeri* and *Carex aquatilis* were the arctic tundra species examined. *Deschampsia* and *Dupontia* are typically found in wet meadow habitats, whereas *Geum* and *Carex* cover a wider range of habitats from wet meadows to somewhat drier, more exposed areas in their respective tundras. A thorough characterization of the tundra areas where these plants were obtained as well as the laboratory growth techniques are presented in Chapter II.

Laboratory gas exchange measurements were conducted using two Siemens Corp. Sirigor gas exchange systems (Koch, Lange, and Schulze, 1971). Irradiation was provided by four Sylvania 300-W incandescent lamps, and total quanta between 400 and 700 nm were measured with a Lambda Model LI-190 SR quantum sensor. Leaf temperatures were measured with fine-wire copper-constantan thermocouples, and an air stream conditioning system combined with a vapor trap bypass was used to control cuvette water vapor pressure. Water vapor concentrations were measured with Cambridge Model 880 dewpoint hygrometers, while a Beckman Model 215 infrared gas analyzer measured CO_2 differentials.

Leaf areas (one side) were determined using a Lambda Model LI-3000 portable area meter and subsequent dry weight determinations were made after allowing the leaf samples to dry at 90°C for 18 hr. Resistances to CO_2 uptake were calculated according to Gaastra (1959) as described in Chapter I. Stomatal diffusion resistance, r'_s, as used in this study includes a leaf boundary layer resistance, r'_a, which was considered to be small for these microphyllous plants under conditions of rapid convection ($\simeq 1\ m \cdot sec^{-1}$) in the gas exchange cuvettes. For example, using convective coefficients of Gates and Papian (1971), at this convection level, r_a would be less than $0.1\ sec \cdot cm^{-1}$ for these tundra species.

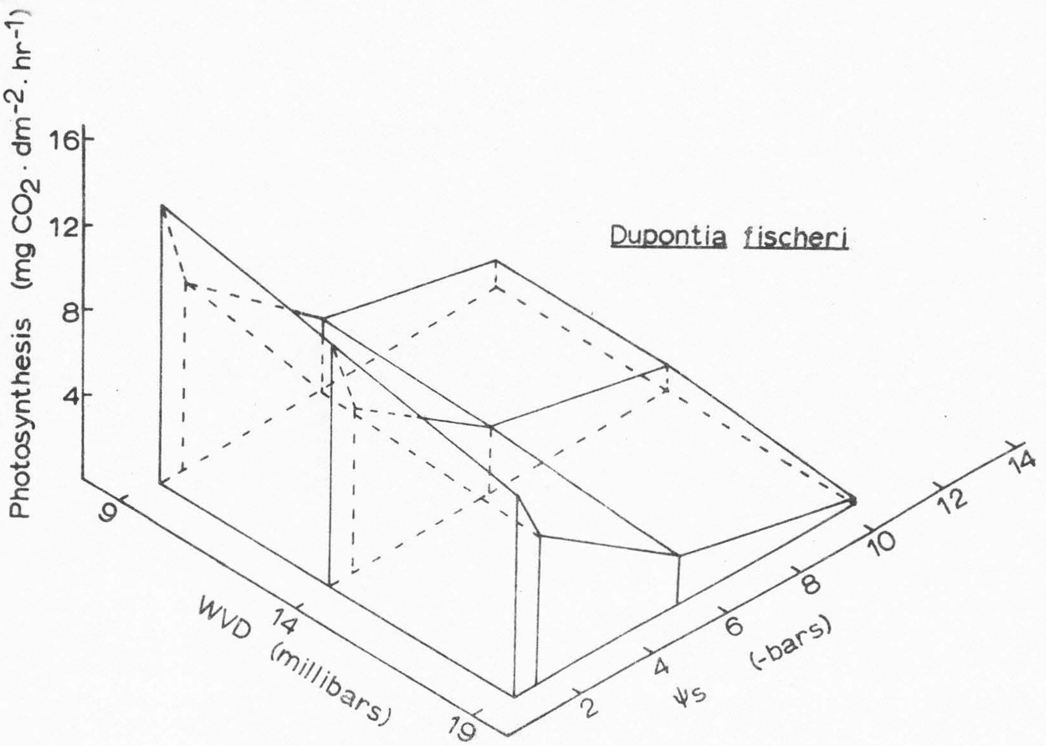
The desired soil moisture levels were obtained by withholding water from the potted plants. A drying period of approximately 6 days was required to obtain the lowest soil moisture levels used in this study. So as not to confound the experiment by introducing long-term effects of plant exposure to a low soil moisture level, plants that were used for a low soil moisture experiment were not used for subsequent experiments. The term WVD used in this study refers to water vapor difference between saturated internal leaf vapor pressure and cuvette air vapor pressure. The sequence of WVD exposure was varied for each plant, thus minimizing any residual carryover effect caused by using the same WVD sequence. Leaf water potentials of each leaf sealed within the cuvette were determined immediately after their removal from the cuvette using a Scholander-type pressure chamber (Waring and Cleary, 1967). After leaf removal, soil water status of the potted plant was determined using either <u>in situ</u> soil psychrometers or a Wescor Model C-52 psychrometer assembly which allows soil samples to be placed into a sample holder and sealed in an airtight aluminum chamber. Three replicates were taken from each pot. A constant saturating light intensity of 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ and a constant leaf temperature of 20°C were maintained during subsequent moisture stress experiments.

Results

All relationships discussed in this section are statistically significant at the .95 level. In addition, standard deviation ranges are presented in the figure legends. The effect of increasing atmospheric stress (increasing WVD) and increasing soil moisture stress (decreasing Ψ_s) on net photosynthesis was investigated for each species (Figures 9 and 10). Striking differences were noted between the wet site species, Deschampsia and Dupontia, and the wider ranging species, Geum and Carex. At the lowest atmospheric and soil moisture stress levels, Deschampsia and Dupontia exhibited rates of 17 and 13 mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$, respectively; whereas, Geum and Carex had rates of only 12 and 9 $mg \cdot dm^{-2} \cdot hr^{-1}$, respectively.

Another striking difference between the wet site and more widely distributed species can be noted in the relationship of net photosynthesis and Ψ_s. Deschampsia and Dupontia exhibited earlier declines in net photosynthesis as Ψ_s decreased than did Geum and Carex. For example, near Ψ_s of -8 bars and low WVD, net photosynthetic rates of Deschampsia and Dupontia had declined to values less than 10 percent of maximal rates. However, Geum and Carex under comparable conditions still exhibited photosynthetic values near 65 percent and 30 percent of their maximum values, respectively.

Figure 9. Net photosynthesis of *Dupontia fischeri* and *Carex aquatilis* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. For *Dupontia* ± one standard deviation ranged from 2.9 at high Ψ_s to 0.1 at low Ψ_s; whereas, ± one standard deviation for *Carex* ranged from 2.5 at high Ψ_s to 0.8 at low Ψ_s.


Dupontia fischeri
Photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
16
12
8
4
WVD (millibars)
9
14
19
ψ_s (-bars)
2
4
6
8
10
12
14

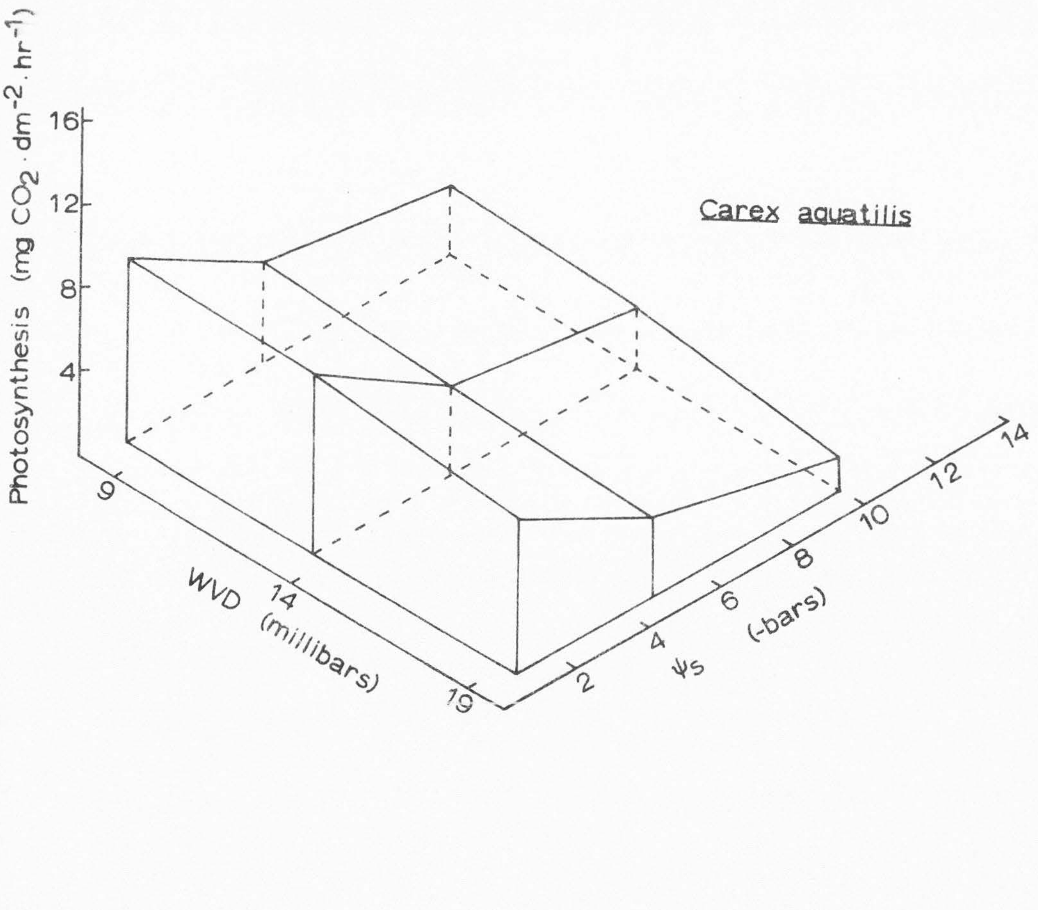
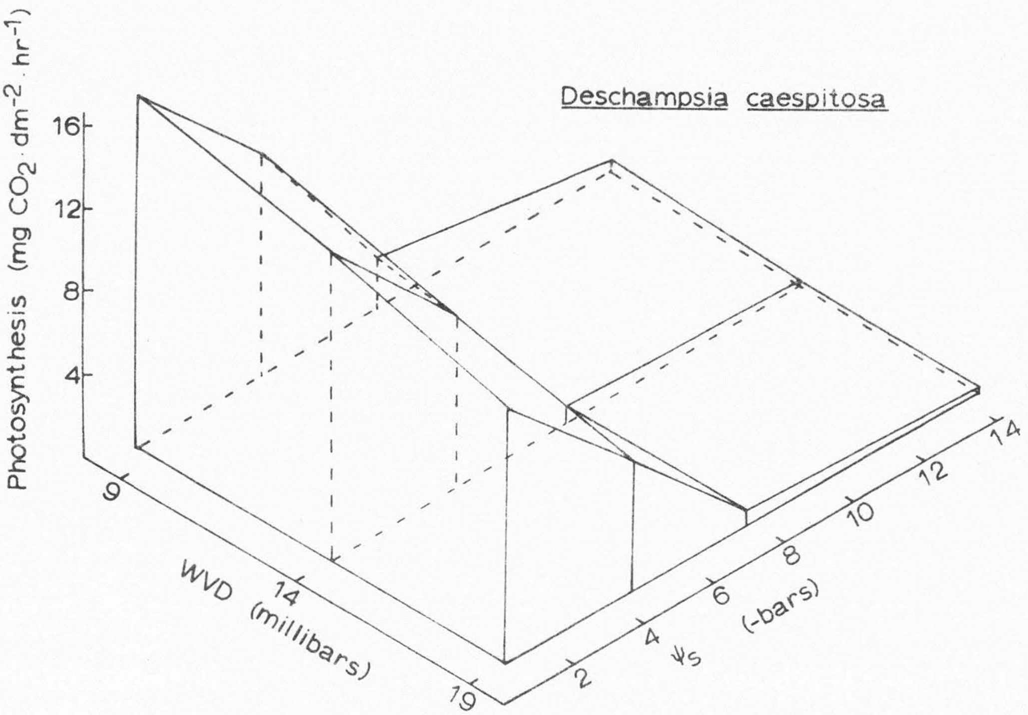
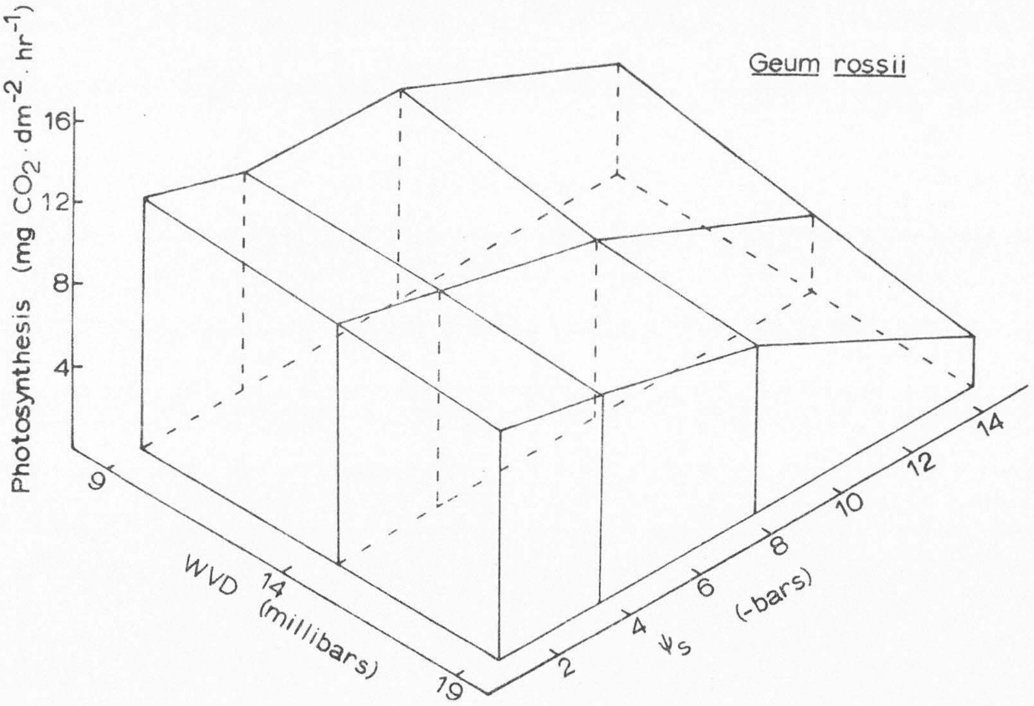

Carex aquatilis
Photosynthesis (mg $CO_2 \cdot dm^{-2} \cdot hr^{-1}$)
16
12
8
4
WVD (millibars)
9
14
19
ψ_s (-bars)
2
4
6
8
10
12
14

Figure 10. Net photosynthesis of *Deschampsia caespitosa* and *Geum rossii* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. For *Deschampsia* ± one standard deviation ranged from 2.9 at high Ψ_s to 0.1 at low Ψ_s; whereas ± one standard deviation for *Geum* ranged from 3.2 at high Ψ_s to 0.8 at low Ψ_s.


Deschampsia caespitosa
Photosynthesis (mg CO$_2$ · dm^{-2} · hr^{-1})
16
12
8
4
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_s (-bars)


Geum rossii
Photosynthesis (mg CO$_2$ · dm^{-2} · hr^{-1})
16
12
8
4
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_s (-bars)

Although alpine species exhibited lower stomatal resistances, r'_s, than arctic species, species with similar habitat distributions from each of the tundra areas showed similar responses (Figures 11 and 12). An important difference between the wet site and the wider ranging species can be noted in comparing their residual resistance, r'_r. Under high Ψ_s and low WVD the wider ranging species in both the arctic and alpine tundras had significantly higher r'_r as compared with the wet meadow species; Carex and Geum exhibited values of 16 and 13 $sec \cdot cm^{-1}$, respectively, as compared with 8 and 9 $sec \cdot cm^{-1}$ for Dupontia and Deschampsia.

All four species exhibited increases in r'_s with increasing WVD levels under high Ψ_s conditions. Carex exhibited the largest increase, followed by Dupontia, Geum and Deschampsia. Associated with these differences in stomatal resistance were differences in residual resistance response. At high Ψ_s both Deschampsia and Dupontia exhibited significant increases in r'_r as WVD proceeded from low to high levels, whereas r'_r for the wider ranging species, Geum and Carex, did not undergo a statistically significant increase.

Significant declines in leaf water potentials, Ψ_1, were associated with these increased r'_r in Deschampsia and Dupontia. As atmospheric stress increased from 9 to 19 mb, Ψ_1 of Dupontia decreased from -19 to -21 bars. Similarly, Deschampsia Ψ_1 declined from -11 to -12 bars. This is in contrast to the wider ranging species where no statistically significant decline in Ψ_1 was observed.

The effects of WVD and Ψ_s on the component CO_2 resistances are presented in Figures 13 and 14. In all species the largest component

Figure 11. Leaf (shaded top layer) and residual (unshaded bottom layer) resistances to CO_2 transfer of _Dupontia fischeri_ and _Carex aquatilis_ as a function of WVD at a leaf temperature of 20°C, 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated and a Ψ_s of near -1 bar. Each point represents the mean of 8 replicates. Stomatal resistance ± one standard deviation ranged from 0.5 to 2.1 for _Dupontia_ and 1.0 to 3.6 for _Carex_.

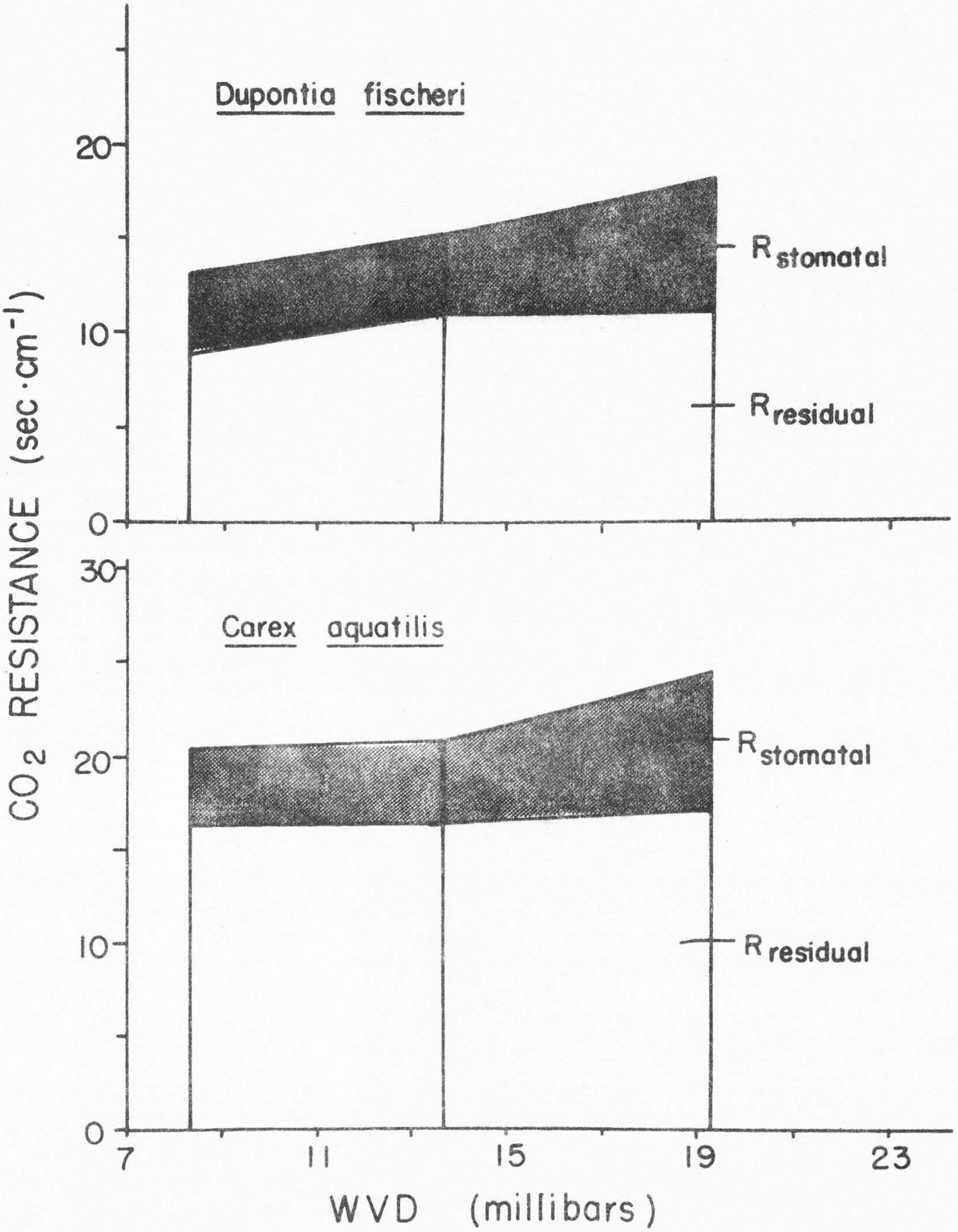

Dupontia fischeri
R stomatal
R residual
Carex aquatilis
R stomatal
R residual
CO2 RESISTANCE (sec·cm⁻¹)
0
10
20
30
0
10
20
7
11
15
19
23
WVD (millibars)

Figure 12. Leaf (shaded top layer) and residual (unshaded bottom layer) resistances to CO_2 transfer of *Deschampsia caespitosa* and *Geum rossii* as a function of WVD at a leaf temperature of 20°C, 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400 to 700 nm) where photosynthesis was light-saturated and a Ψ_s of near -1 bar. Each point represents the mean of 8 replicates. Stomatal resistance ± one standard deviation ranged from 0.3 to 0.7 for *Deschampsia* and 0.4 to 1.6 for *Geum*.

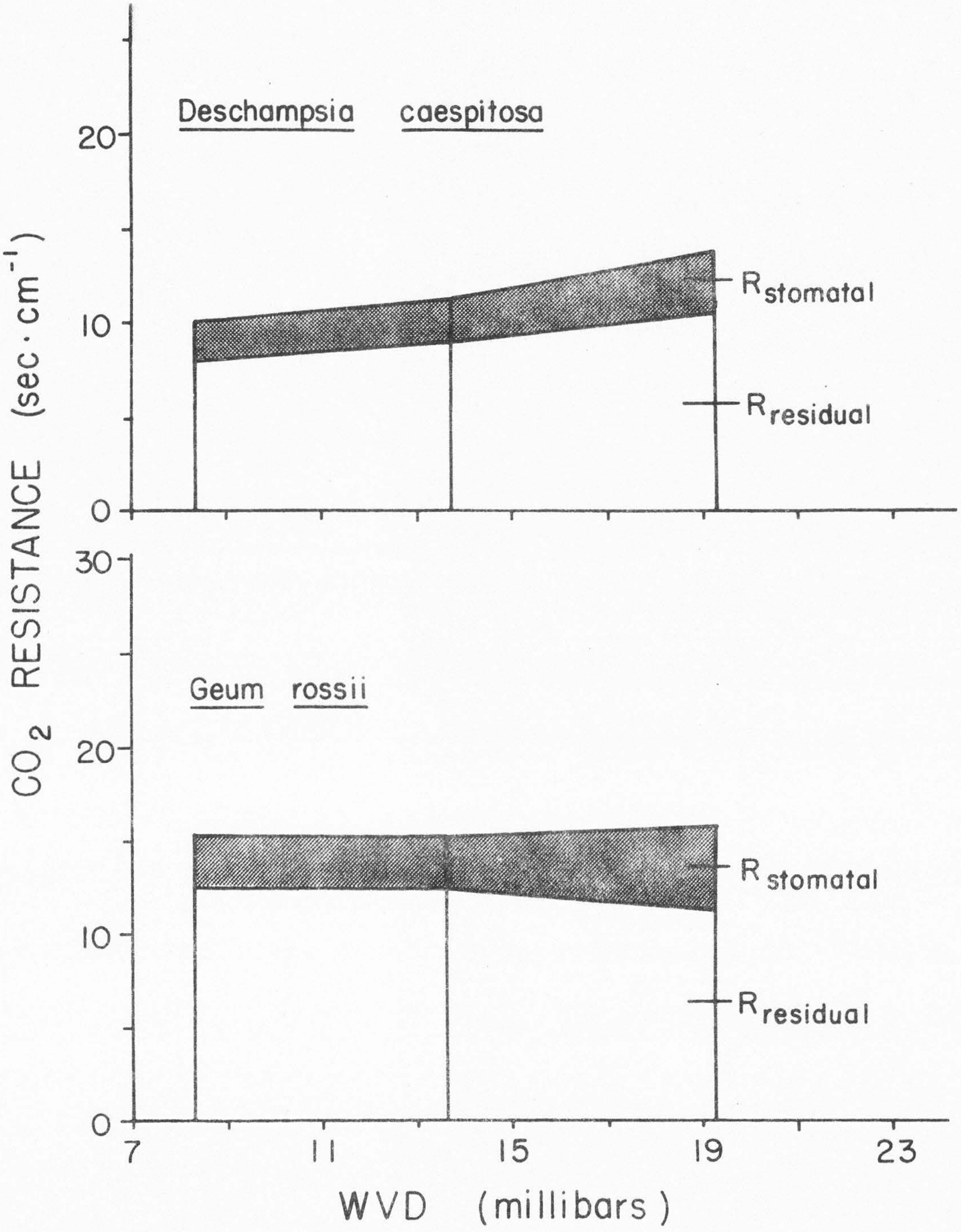
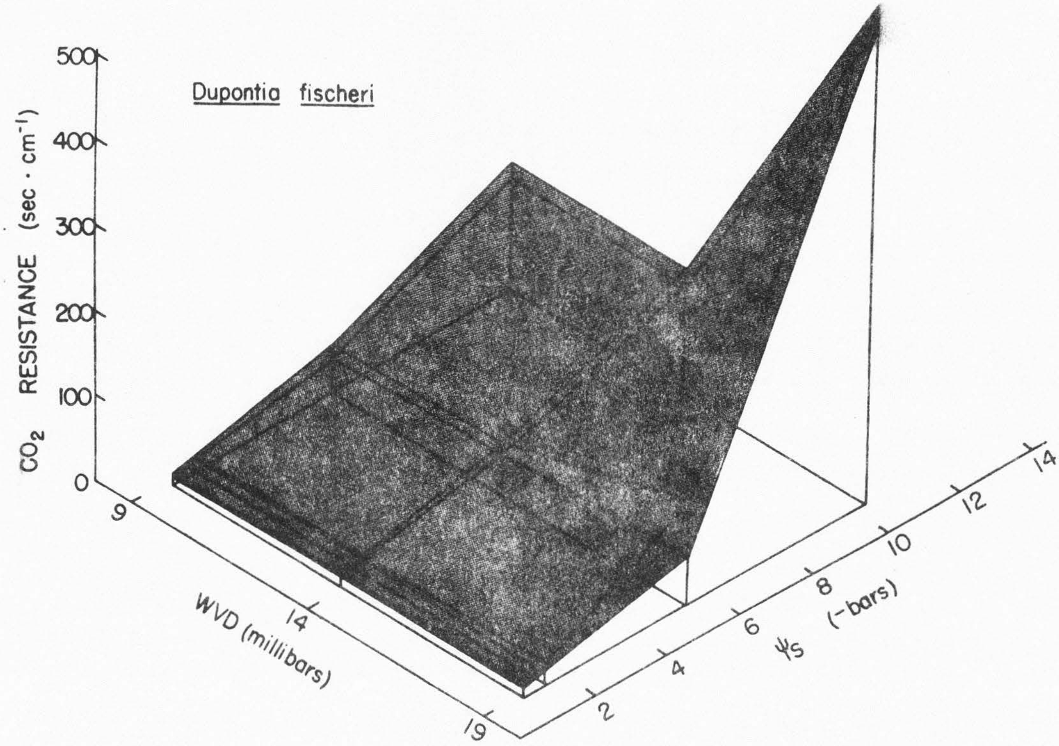

Deschampsia caespitosa
20
10
0
R stomatal
R residual
30
Geum rossii
20
10
0
R stomatal
R residual
7
11
15
19
23
WVD (millibars)
CO2 RESISTANCE (sec · cm⁻¹)

Figure 13. Leaf (shaded top layer) and residual (unshaded bottom layer) resistances to CO_2 transfer of Dupontia fischeri and Carex aquatilis as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point represents the mean of 4 to 8 replicates. For Dupontia stomatal resistance ± one standard deviation ranged from 0.5 at high Ψ_s to 74.8 at low Ψ_s; whereas, residual resistance ± one standard deviation ranged from 2.5 at high Ψ_s to 731.6 at low Ψ_s. For Carex stomatal resistance ± one standard deviation ranged from 1.0 at high Ψ_s to 3.3 at low Ψ_s; whereas, residual resistance ± one standard deviation ranged from 2.9 at high Ψ_s to 21.2 at low Ψ_s.


Dupontia fischeri
CO$_2$ RESISTANCE (sec · cm^{-1})
500
400
300
200
100
0
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_s (-bars)

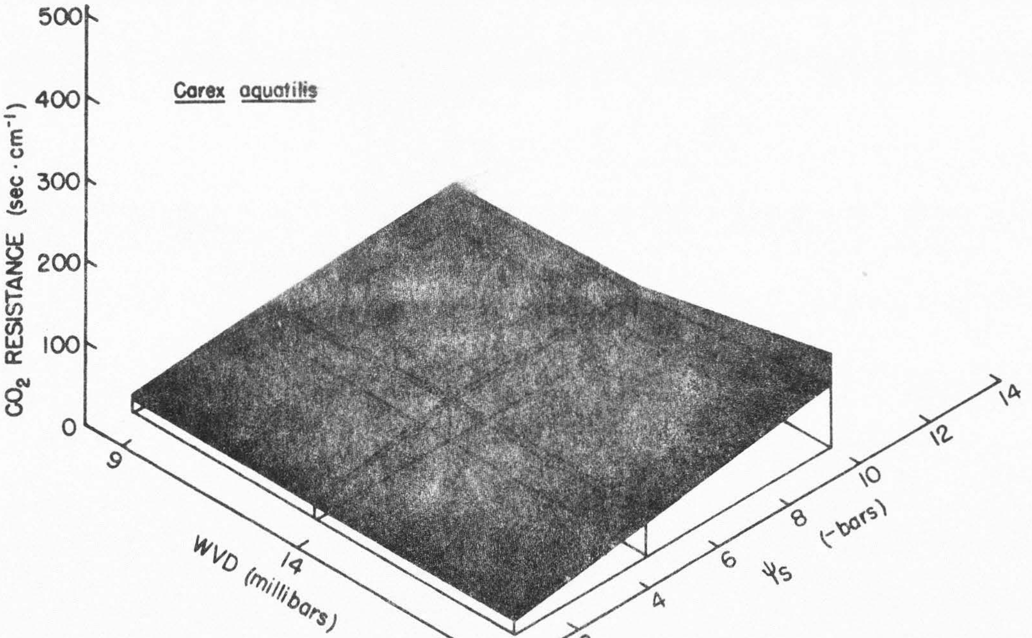
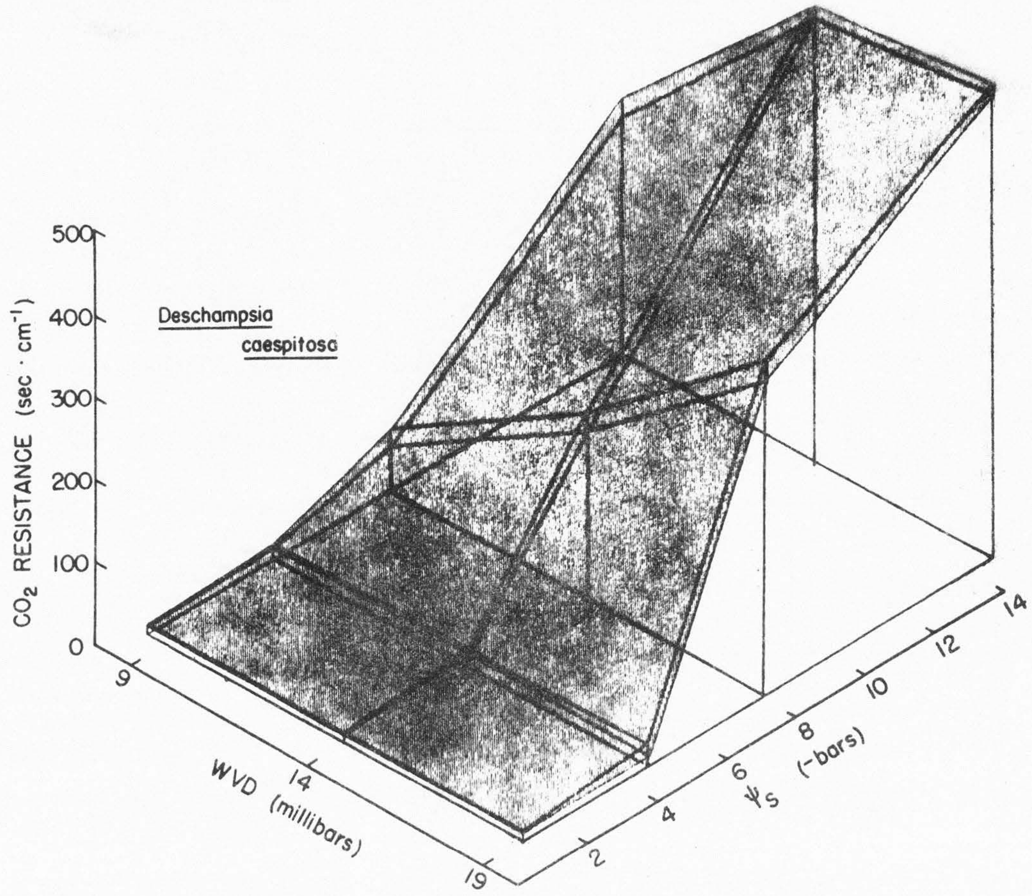
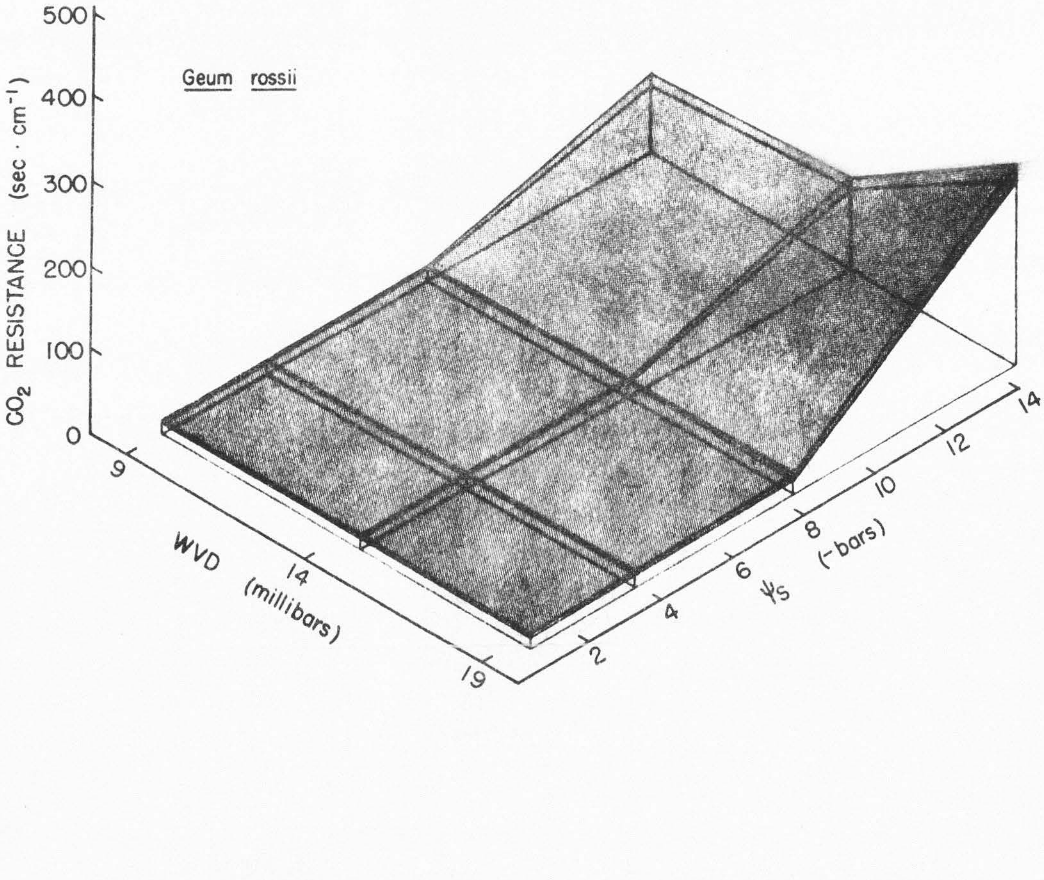

Carex aquatilis
CO$_2$ RESISTANCE (sec · cm^{-1})
500
400
300
200
100
0
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_s (-bars)

Figure 14. Leaf (shaded top layer) and residual (unshaded bottom layer) resistances to CO_2 transfer of *Deschampsia caespitosa* and *Geum rossii* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point represents the mean of 4 to 8 replicates. For *Deschampsia* stomatal resistance ± one standard deviation ranged from 0.3 at high Ψ_s to 8.4 at low Ψ_s; whereas, residual resistance ± one standard deviation ranged from 1.5 at high Ψ_s to 944.1 at low Ψ_s. For *Geum* stomatal resistance ± one standard deviation ranged from 0.4 at high Ψ_s to 10.2 at low Ψ_s; whereas, residual resistance ± one standard deviation ranged from 2.7 at high Ψ_s to 275.2 at low Ψ_s.


Deschampsia caespitosa
CO$_2$ RESISTANCE (sec · cm^{-1})
500
400
300
200
100
0
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_S (-bars)


Geum rossii
CO$_2$ RESISTANCE (sec · cm^{-1})
500
400
300
200
100
0
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψ_S (-bars)

resistance was r'_r. However, as noted earlier, r'_s, was an important controlling resistance at the higher Ψ_s levels. A general pattern of increasing r'_r with decreasing Ψ_s was exhibited by all four species. However, the wet site species, Deschampsia and Dupontia, exhibited an earlier, sharper rise in r'_r as compared to the wider ranging species, Geum and Carex. For example, in Deschampsia and Dupontia r'_r reached 80 $\mathrm{sec \cdot cm^{-1}}$ before Ψ_s dropped to -6 bars. However, these high r'_r were not exhibited in Geum and Carex until Ψ_s approached -10 bars.

Since r'_r as calculated in this study includes respiratory CO_2 loss, the effect of increasing soil moisture stress upon dark respiration was investigated (Figures 15 and 16). In all four species there were no statistically significant increases in dark respiratory rates as soil moisture stress increased. In fact, as Ψ_s declined, there was a statistically significant decrease in respiration of Dupontia. Thus, the marked increases in the r'_r noted in all four species as Ψ_s was lowered was not likely due to increased mitochondrial respiration as can be assayed in the dark. There remains, however, the possibility that photorespiration may increase when water stress intensifies (Ludwig and Canvin, 1971b).

Water use efficiencies which are taken as photosynthesis/ transpiration ratios are presented in Figures 17 and 18. The wet site species, Dupontia and Deschampsia, exhibited higher water use efficiencies for photosynthesis at high Ψ_s levels; however, as Ψ_s decreased, the water use efficiencies of Carex and Geum exceeded those of the wet site species.

Figure 15. Dark respiration CO_2 losses of *Dupontia fischeri* and *Carex aquatilis* at a high (●) and low (X) Ψ_s as a function of leaf temperature. Each point represents the mean of 4 replicates with associated ± one standard deviation.

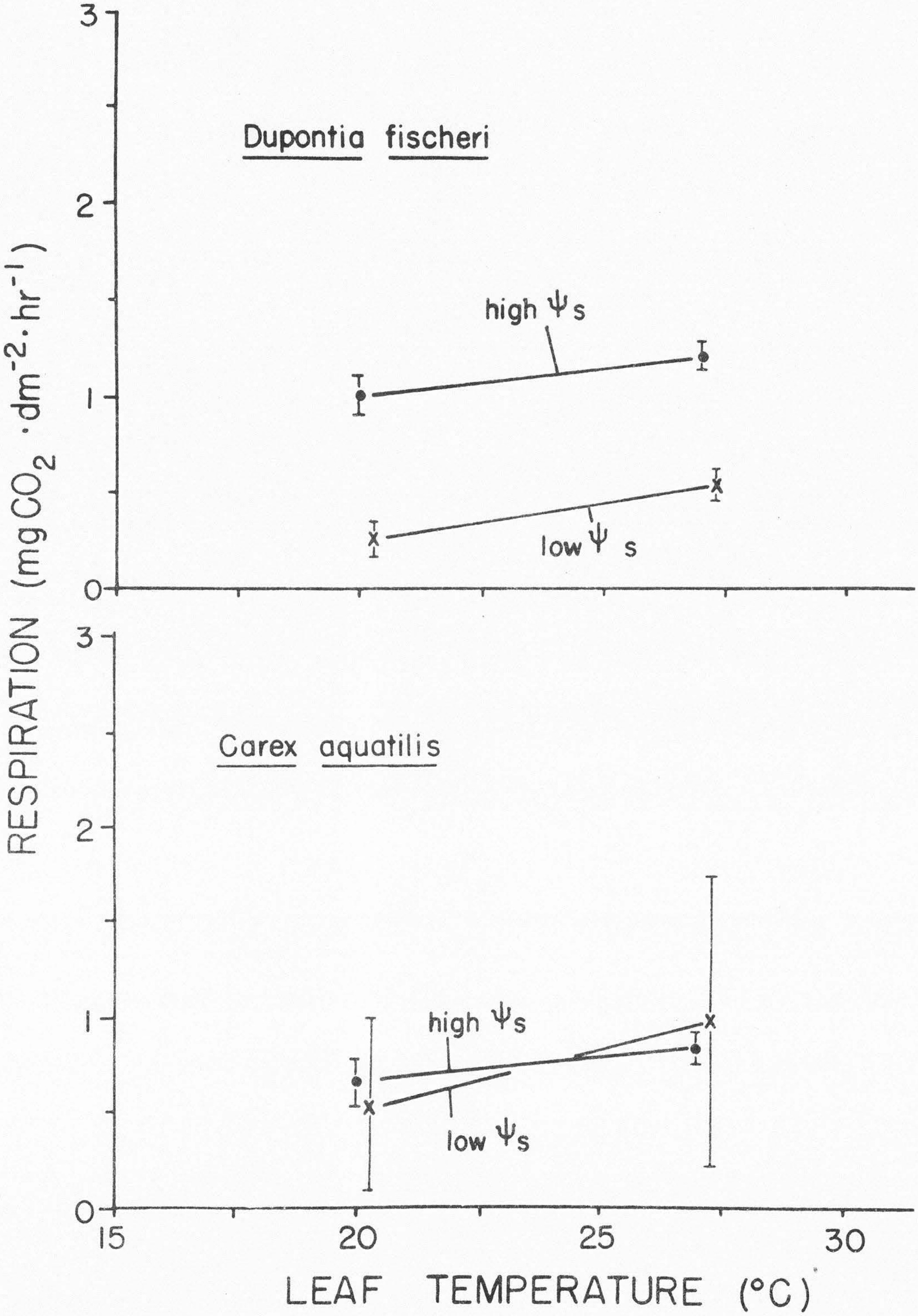

Dupontia fischeri
high Ψs
low Ψ s
Carex aquatilis
high Ψs
low Ψs
RESPIRATION (mg CO$_2$ ·dm^{-2}·hr^{-1})
0
1
2
3
0
1
2
3
15
20
25
30
LEAF TEMPERATURE (°C)

Figure 16. Dark respiration CO_2 losses of *Deschampsia caespitosa* and *Geum rossii* at a high (●) and low (X) Ψ_s as a function of leaf temperature. Each point represents the mean of 4 replicates with associated ± one standard deviation.

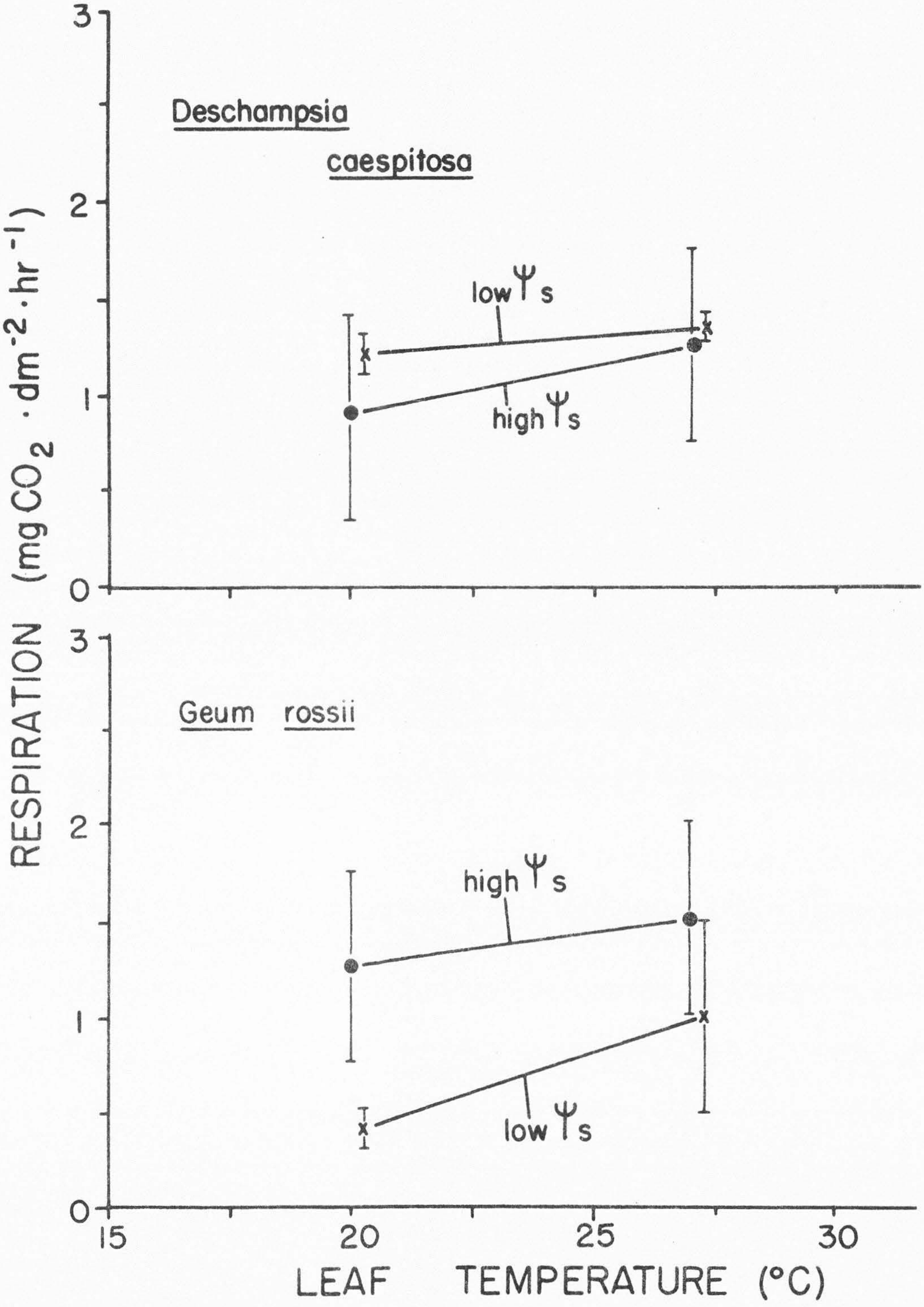
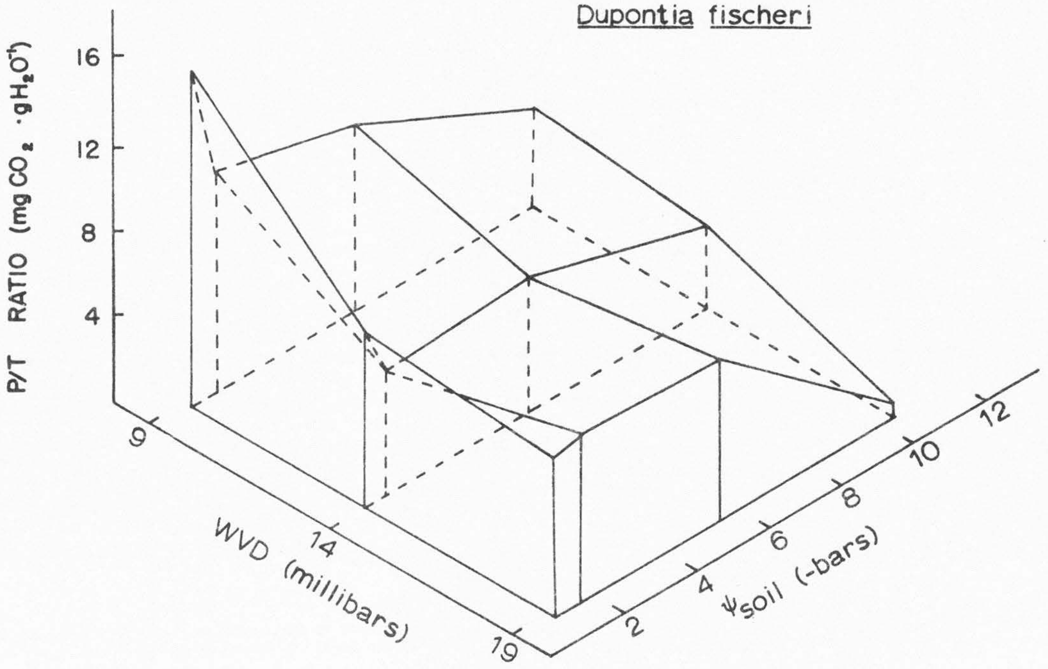
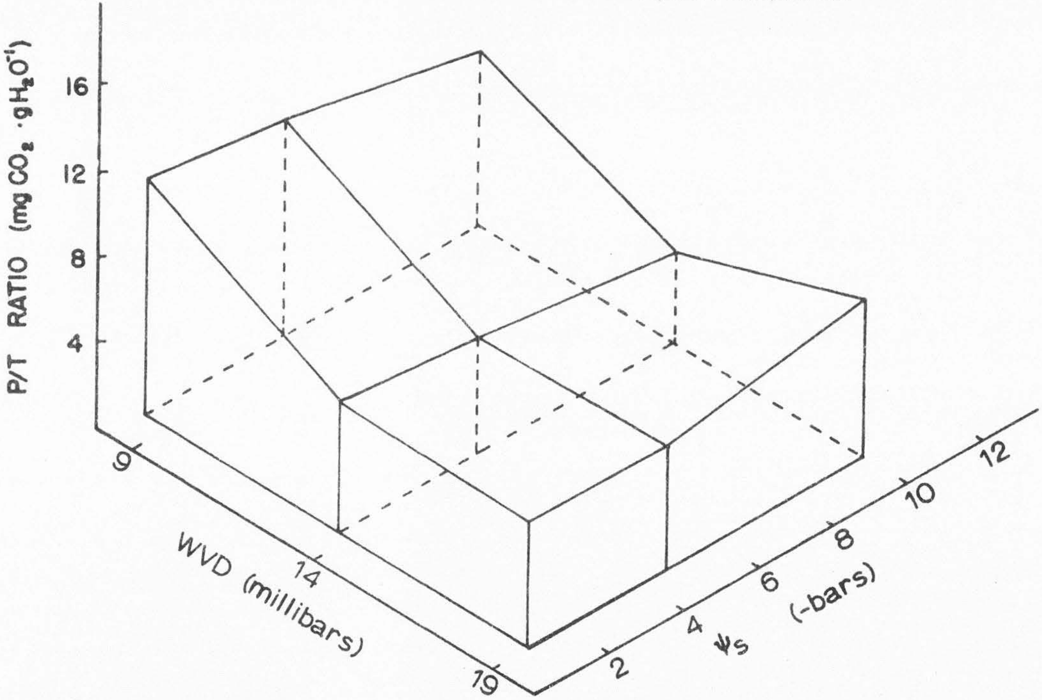

Deschampsia caespitosa
low Ψ_s
high Ψ_s
Geum rossii
high Ψ_s
low Ψ_s
RESPIRATION (mg CO$_2$ · dm^{-2} · hr^{-1})
0
1
2
3
0
1
2
3
15
20
25
30
LEAF TEMPERATURE (°C)

Figure 17. Photosynthesis/transpiration ratios of *Dupontia fischeri* and *Carex aquatilis* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. For *Dupontia* ± one standard deviation ranged from 5.8 to high Ψ_s to 0.1 at low Ψ_s; whereas, ± one standard deviation for *Carex* ranged from 5.0 at high Ψ_s down to 1.4 at low Ψ_s.

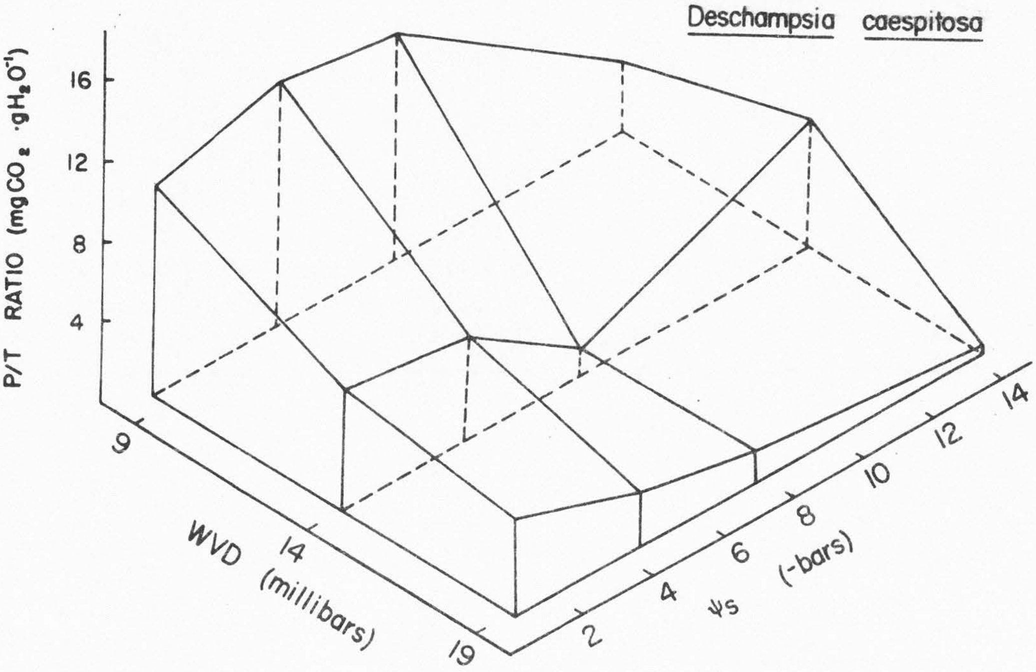


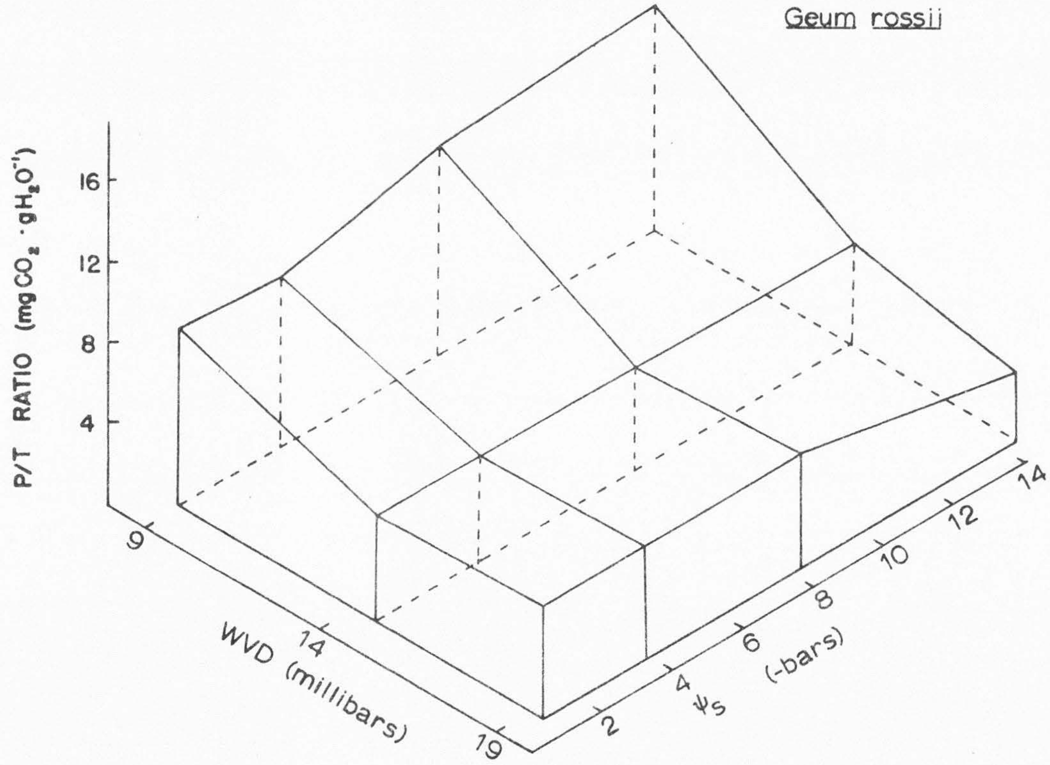
Dupontia fischeri



Carex aquatilis

Figure 18. Photosynthesis/transpiration ratios of *Deschampsia caespitosa* and *Geum rossii* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. For *Deschampsia* ± one standard deviation ranged from 5.2 at high Ψ_s to 0.4 at low Ψ_s; whereas ± one standard deviation for *Geum* ranged from 4.2 at high Ψ_s to 0.7 at low Ψ_s.


Deschampsia caespitosa
P/T RATIO (mgCO₂ · gH₂O⁻¹)
16
12
8
4
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψs (-bars)


Geum rossii
P/T RATIO (mgCO₂ · gH₂O⁻¹)
16
12
8
4
9
14
19
WVD (millibars)
2
4
6
8
10
12
14
ψs (-bars)

Discussion

Depression of photosynthesis due to increasing water stress has been well established for a wide range of plant species (Slatyer, 1967; Kramer, 1969; Kozlowski, 1972; Hsiao, 1973). The tundra species examined in this study also showed a general decline in photosynthetic capacity as water stress increased; however, there were important differences between the wet site species, Dupontia and Deschampsia, and the more widely distributed species, Carex and Geum. The photosynthetic capacities of the wet site species were higher than those of the wider ranging species under conditions of low soil moisture stress. However, this trend was offset by the ability of the wider ranging species to maintain greater photosynthetic capacity as water stress increased (Figures 9 and 10).

These trends would suggest that given an unstressed soil moisture condition, the wet site species would exhibit higher carbon gain per unit leaf material than the wider ranging species in the wet microsites. However, in the more exposed habitats or during particularly dry years, species such as Carex and Geum would be able to maintain a more favorable carbon gain per unit leaf area. This general pattern would, of course, be tempered by a number of other factors including the number of leaves produced as well as the productive period for each leaf. For example, Geum typically exserts about 10 leaves per growing season, whereas Deschampsia typically produces up to 5 leaves (Johnson and Caldwell, 1974).

There is considerable evidence which demonstrates that for many species, declines in photosynthesis with increasing water stress are due principally to increased stomatal resistances, r'_s (e.g., Troughton, 1969; Pasternak and Wilson, 1973). However, additional evidence has been accumulating which suggests that the residual resistance component, r'_r, may also be important in explaining a substanial degree of the photosynthetic depression (Gale, Kohl, and Hagan, 1966; Boyer and Bowen, 1970; Redshaw and Meidner, 1972; DePuit and Caldwell, 1975).

The importance of both r'_s and r'_r in explaining photosynthetic declines with increasing water stress is apparent from the results of this study (Figures 11, 12, 13, and 14). In all four species, r'_r comprised the largest component of the total resistance to CO_2 uptake under any combination of atmospheric and soil moisture stress. Although declines in photosynthesis were associated with both r'_s and r'_r as Ψ_s decreased, r'_r typically showed the largest increase. However, when Ψ_s was greater than -5 bars, r'_s usually showed the largest increase and generally exerted the controlling influence in depressing photosynthetic rates. It is apparent that either r'_s or r'_r can be the primary resistance responsible for photosynthetic decline depending on the particular set of conditions. These results suggest that extrapolations of photosynthesis from only r'_s measurements as has been done for other alpine tundra species (Ehleringer and Miller, 1975) may be somewhat tenuous.

At some point in the series of decreasing Ψ_s levels, r'_r increased sharply resulting in large declines in photosynthesis for all species studied. The wet site species from both tundra areas exhibited this marked increase in r'_r at significantly higher Ψ_s

than the wider ranging species from both the alpine and arctic sites. These increases in r'_r might be partially attributed to increases in respiratory CO_2 loss. Increased dark respiration has been found for some arid and Mediterranean species under high moisture stress (e.g., Mooney, 1969; DePuit and Caldwell, 1975). However, the results from this study indicate that this is not the case for these tundra species. Dark respiration did not increase with water stress (Figures 15 and 16) which is in agreement with reports for other species (e.g., Greenway and Hiller, 1967; Boyer, 1971). These results suggest that the sharp increases in r'_r may involve other causes such as increased photorespiration, alterations of membrane integrity, chloroplast disruption, or enzyme function (e.g., Ludwig and Canvin, 1971; Parker, 1972). Although normal mitochrondrial respiration as assayed in the dark may be somewhat depressed when the plant is in the light (Jackson and Volk, 1970), at least part of the respiratory CO_2 losses from leaves in the light may be indicated by dark respiration rates. Photorespiration has not been assessed in this study and may behave quite differently than dark respiration when these plants are under water stress.

Under high Ψ_s, increasing atmospheric moisture stress resulted in decreased photosynthetic capacities to a greater extent in the wet site species than in the wider ranging species. Even though all four species exhibited some increase in r'_s, only the wet site species showed a concomitant increase in r'_r. The increased r'_r and r'_s in the wet site species were associated with decreases in leaf water status. Thus, not only might the increase in r'_r be attributed to lowered Ψ_1, but increased r'_s might also have resulted simply from a hydropassive reduction in stomatal aperture resulting from changes in bulk leaf water status. Such hydropassive stomatal mechanisms have been well established for some crop species (e.g., Kanemasu and Tanner, 1969; Duniway and Durbin, 1971).

In contrast, the wider ranging species exhibited no significant increase in r'_r and associated declines in leaf water status. Thus, the stomatal mechanism of the wider ranging species may have responded directly to the WVD gradient and hence prevented changes in the bulk leaf water status. This has been reported in a variety of other species by Lange et al. (1971), Schulze et al. (1972), Comacho-B et al. (1974), and Hall and Kaufmann (1975). This mechanism might have allowed a particularly significant stomatal occlusion in leaves of Carex which in turn abetted maintenance of pre-stress leaf water status. A more moderate increase in r'_s in Geum, the other wider ranging species, suggests that additional factors may have played a significant role in maintaining Ψ_1 in this species. Other studies, for example, have shown that Geum exhibits a lower liquid-phase resistance to water transport in the plant than the other three species and will be discussed in detail in Chapter V.

Lange et al. (1971) have proposed that the mechanism of rapid stomatal response to WVD gradients may involve peristomatal transpiration where guard cells may respond directly to changes in leaf-to-atmosphere vapor pressure gradients through effects of turgor on guard cell walls. This response mechanism may provide an adaptive advantage for these wider ranging species in restricting water loss and thereby preventing the development of water stress within the mesophyll tissues of the leaf. This would allow a more sensitive mechanism for stomatal closure in these wider ranging species than the apparent hydropassive stomatal mechanism of the wet site species.

The wet site species typically exhibited higher water use efficiencies at high Ψ_s; however, as Ψ_s decreased, water use efficiency of the wider ranging species exceeded those of the wet site species (Figures 17 and 18). Although reduced stomatal aperture increased water use efficiency in all of the species, since r'_r comprises such a large portion of the total CO_2 uptake resistance for these plants, it also necessarily plays a large role in determining their water use efficiency.

If this water use efficiency for photosynthesis corresponds to water use efficiency for growth in the field, the differences in efficiency between species could be an important factor in partially explaining distribution patterns of these tundra species. The wet site species may have evolved mechanisms which contribute to high photosynthetic rates under wet meadow conditions. At the same time this specialization may have restricted the ability of these wet site species to maintain photosynthetic carbon gain at appreciable levels under moisture stress. This is in contrast to the wider ranging species which appear to have a more generalized strategy. Although photosynthetic rates of *Geum* and *Carex* are not as high under favorable moisture conditions, they are able to maintain higher photosynthetic rates over a wider range of soil moisture regimes.

The results of this study show that tundra plants exhibit different gas exchange behavior with respect to moisture stress and suggest that these responses may be one important contributing factor in determining the microsite distributions of these species in tundra areas.

CHAPTER V

LABORATORY WATER RELATIONS STUDY

Introduction

Although not all habitats within tundra environments are constantly under moisture stress, it seems that plant moisture stress may develop in many years in the more exposed sites and in very dry years may even occur in the more mesic tundra microsites. Consequently, tundra species have likely evolved different physiological adaptations depending upon their local distribution. Indeed, the results discussed in Chapter IV showed that although tundra species restricted to more moist sites have higher net photosynthetic rates under conditions of low moisture stress, their photosynthetic rates declined more rapidly with increasing water stress than those of wider ranging species. Furthermore, these results suggested that additional physiological mechanisms besides leaf diffusive resistances may be involved.

Several authors have noted that other physiological processes such as cell growth may be inhibited at much lower water stress levels than processes such as photosynthesis (e.g., Cleland, 1967; Hsaio, 1973). Thus, even though water stress may not be severe enough to limit primary production through depression of photosynthetic rates in these tundra species, productivity limitation by depressed growth rates may occur more frequently. The investigations reported here were undertaken to determine additional attributes which may be important contributing factors in determining the distributions of tundra species.

Methods

The alpine tundra plant species examined were *Deschampsia caespitosa* and *Geum rossii*, and the arctic tundra species investigated were *Dupontia fischeri* and *Carex aquatilis*. *Deschampsia* and and *Dupontia* are typically found in wet meadow habitats in their respective tundras, whereas *Geum* and *Carex* cover a wider range of habitats from wet meadows to somewhat drier, more exposed areas. A detailed description of the tundra areas where these species were obtained as well as the laboratory growth techniques are presented in Chapter II. In addition, the same gas exchange equipment and techniques as in Chapter IV were used in this study. Water vapor leaf diffusive resistances were calculated as described in Chapter I. Stomatal diffusion resistance, r_s, as used in this study includes a leaf boundary layer resistance, r_a, which was considered to be small for these microphyllous plants under conditions of rapid convection (~1 $m \cdot sec^{-1}$) in the gas exchange cuvettes. For example, using convective coefficients of Gates and Papian (1971), at this convection level r_a would be less than 0.1 $sec \cdot cm^{-1}$ for these tundra species.

The water potential components of leaf discs from the four species were determined under a range of soil moisture conditions using a psychrometric technique described in detail by Brown (1975). Each psychrometer assembly contains two Peltier thermocouple psychrometer junctions mounted in a stainless steel housing.

A leaf disc cutter is incorporated into the psychrometer assembly and thereby minimizes leaf evaporative losses between the time of leaf disc excision and sealing in the psychrometer assembly. After leaf disc excision and sealing, the psychrometer assemblies were placed in a water reservoir which allowed stable temperature conditions. After a temperature and vapor pressure equilibration period of one hour, a switching unit (EMCO Model CU-401) with a Keithley microvoltmeter was used to measure the microvolt output of each psychrometer after a Peltier cooling period of 15 sec. These outputs were converted to Ψ_l from individual psychrometer calibrations against saturated NaCl solutions of known molality.

Immediately after Ψ_l was measured, the intact psychrometer assemblies were frozen to near -40°C. These intact psychrometer assemblies were then allowed to slowly warm to room temperature in order to achieve maximum cellular disruption (Sakai and Yoshida, 1967), and then the psychrometric value was again determined. Subsequent reduction of the data after freezing and thawing resulted in determination of Ψ_π and Ψ_m. Evidence of Noy-Meir and Ginzburg (1969), and Miller (1972) suggests that at high Ψ_l, the Ψ_π component often exceeds Ψ_m, whereas at low Ψ_l, the Ψ_m component may be more dominant. Leaf turgor pressure expressed as Ψ_p can then be calculated from the following equation:

$$\Psi_p = \Psi_l - (\Psi_\pi + \Psi_m) \text{ (bars)} \tag{4}$$

where Ψ_l is leaf water potential, Ψ_π is osmotic potential, and Ψ_m is matric potential.

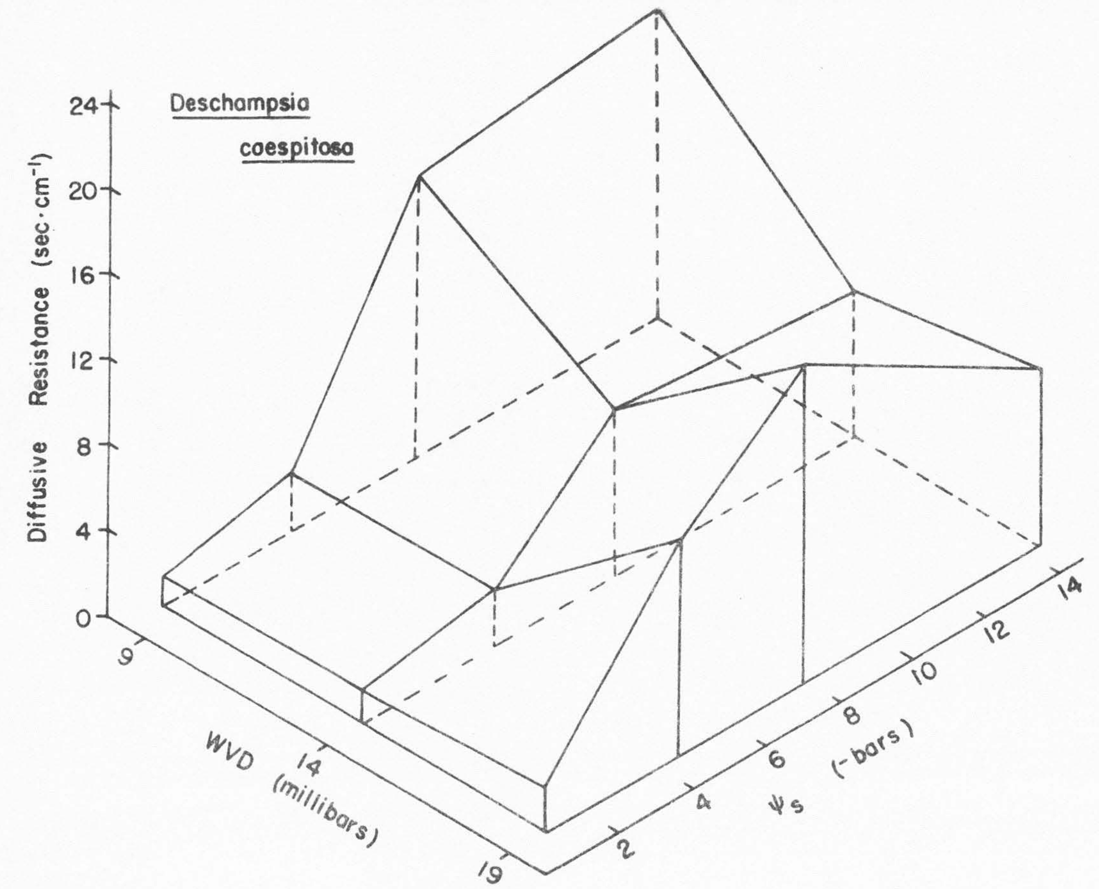
Since the water relations of leaves can change with age and stage of development (Levitt, 1972), only leaves of approximately the same age and vegetative stage were used. The leaves used were the largest, most fully expanded leaves on the plant with the leaf disc samples being take approximately 3 cm from the tip of the leaf.

Results and Discussion

All relationships discussed in this section are statistically significant at the .95 level. The effect of increasing atmospheric stress (increasing WVD) and increasing soil moisture stress (decreasing Ψ_s) on water vapor diffusive resistance, r_s, was investigated for each species (Figures 19 and 20). Although alpine species exhibited lower r_s than the arctic plants, species with similar distributions from each of the tundra areas showed similar responses. Even though all four tundra species exhibited some increase in r_s under high Ψ_s, only the wet site species showed a concomitant decrease in Ψ_l. As suggested in Chapter IV, this increased r_s might have resulted from a hydropassive reduction in stomatal aperture resulting from changes in bulk leaf water status. In contrast, the wider ranging species exhibited no decline in Ψ_l as WVD increased at high Ψ_s. As a result, it was suggested that the stomatal mechanism of the wider ranging species may have responded directly to the WVD gradient and hence prevented changes in the bulk leaf water status.

However, this more sensitive stomatal mechanism in Geum and Carex seems to be overridden as Ψ_s increased. With decreased Ψ_s

Figure 19. Leaf diffusive resistances to water vapor transfer of Dupontia fischeri and Carex aquatilis as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. Leaf diffusive resistance ± one standard deviation ranged from 0.5 at high Ψ_s to 7.5 at low Ψ_s for Dupontia and from 1.0 at high Ψ_s to 3.3 at low Ψ_s for Carex.


Deschampsia coespitosa
Diffusive Resistance (sec·cm⁻¹)
0
4
8
12
16
20
24
WVD (millibars)
9
14
19
ψs (-bars)
2
4
6
8
10
12
14

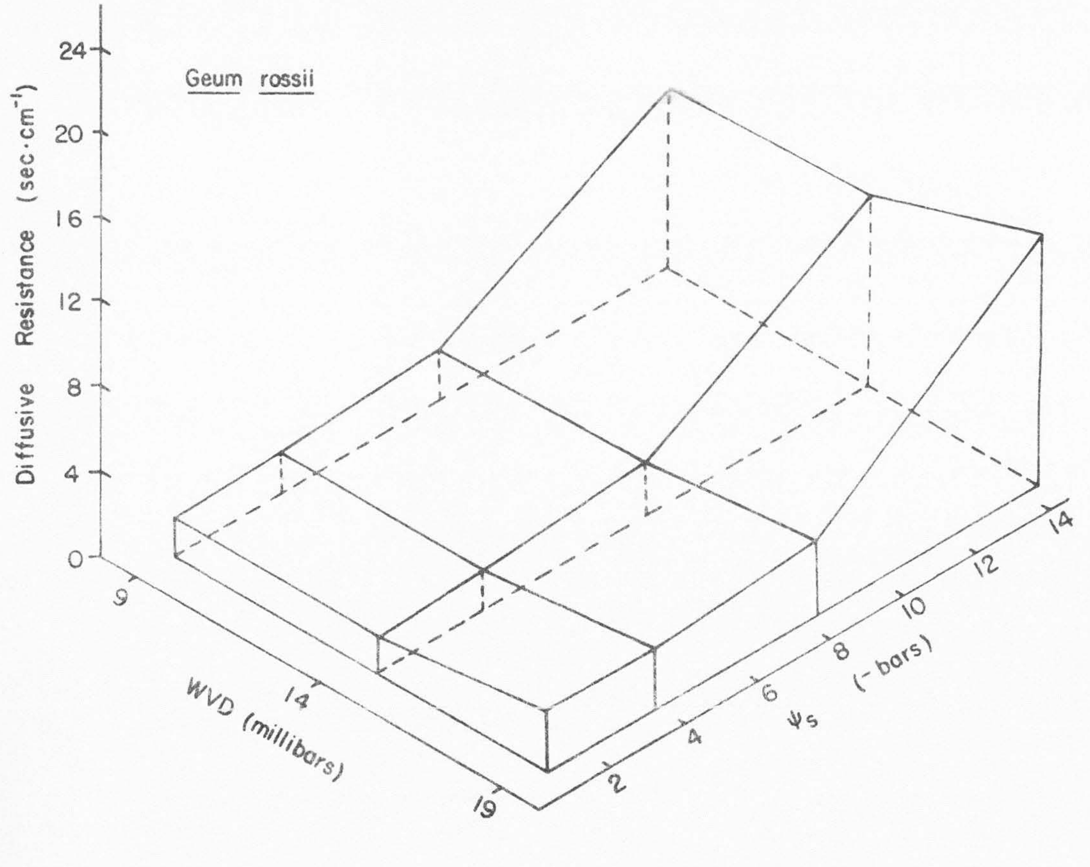
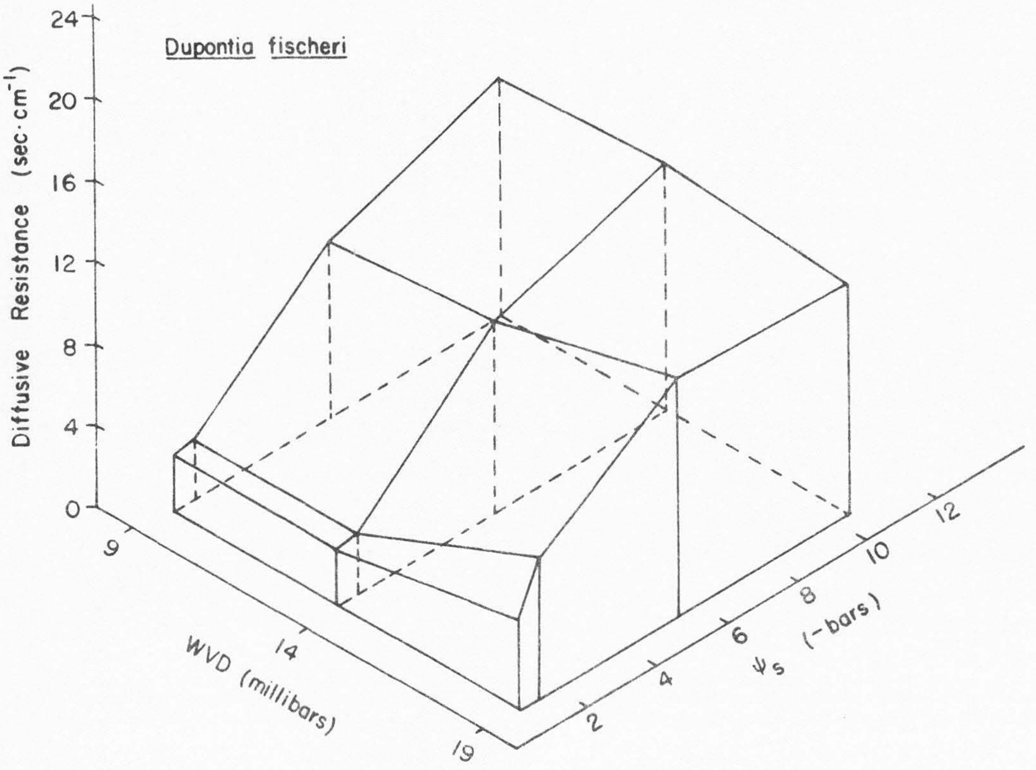
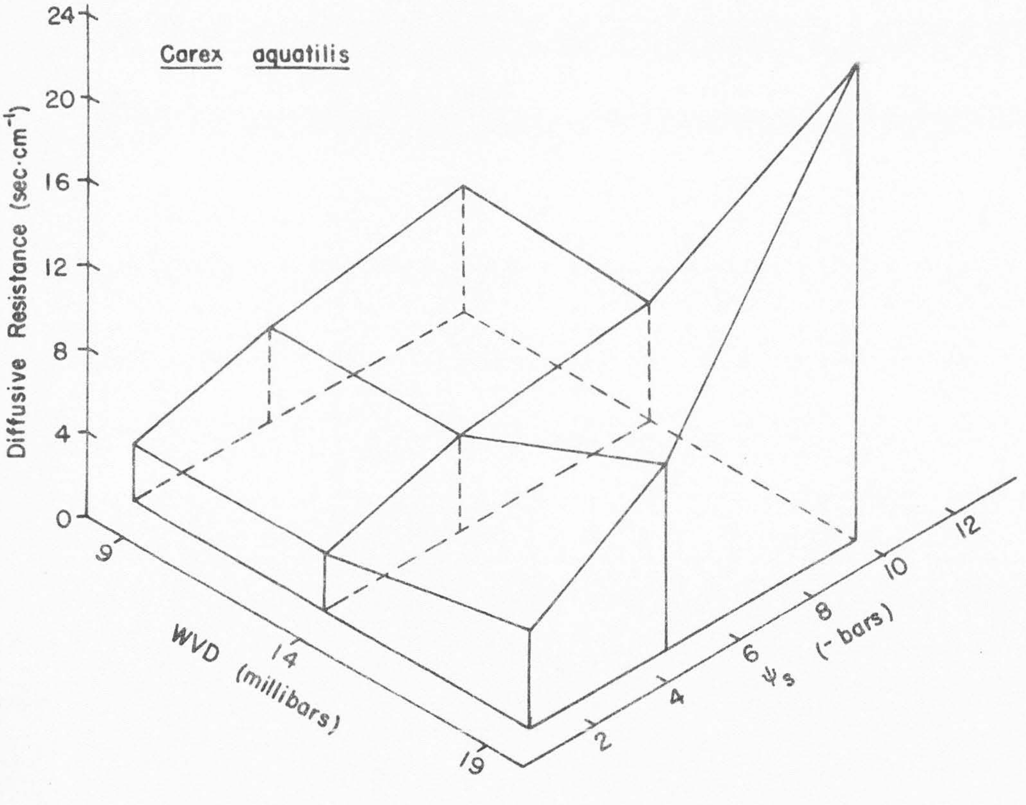

Geum rossii
Diffusive Resistance (sec·cm⁻¹)
0
4
8
12
16
20
24
WVD (millibars)
9
14
19
ψs (-bars)
2
4
6
8
10
12
14

Figure 20. Leaf diffusive resistances to water vapor transfer of *Deschampsia caespitosa* and *Geum rossii* as a function of WVD and Ψ_s at a leaf temperature of 20°C and 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated. Each point on the response surface represents the mean of 4 to 8 replicates. Leaf diffusive resistance ± one standard deviation ranged from 0.3 at high Ψ_s to 8.4 at low Ψ_s for *Deschampsia* and from 0.4 at high Ψ_s to 10.2 at low Ψ_s for *Geum*.



Dupontia fischeri



Carex aquatilis

Carex and especially Geum maintained lower r_s than species typically restricted to wet tundra areas, Dupontia and Deschampsia. As a result, at high Ψ_s the stomata of Geum and Carex seem to respond directly to the WVD gradient, whereas with decreased Ψ_s the stomatal mechanism may respond mainly to changes in bulk leaf water status. These results of greater r_s in species restricted to wet tundra areas are contrary to the results of Mooney, Billings, and Hillier (1965) where broad leaf plants from moist alpine tundra areas in the California Sierra Nevada exhibited little control over transpiration as compared to species from drier sites. Similarly, Ehleringer and Miller (1975) found that broad leaf plants from wet alpine tundra meadow areas on Niwot Ridge in Colorado exhibited higher leaf resistances than the same species growing on drier, more exposed sites. These differences in stomatal response underscore the caution which should be used in extrapolating the results of a few species to a generalization for all species even within a geographically similar area.

The results of this present study seem to suggest that Geum and Carex have mechanisms which allow them to maintain a favorable leaf water balance over a rather broad range of soil moisture regimes. Such a mechanism may be the ability of Geum to maintain a low liquid phase resistance from the soil to the leaf. Indeed, species differences for this resistance term have been found (e.g., Newman, 1969a; Hansen, 1974b). Most of these studies used the generalized equation of van den Honert (1948) as an acceptable approximation for the resistances of water flux through the soil-plant system:

$$R_s + R_p = \frac{\Psi_s - \Psi_1}{T} \quad (\text{bar}\cdot\text{sec}\cdot\text{cm}^{-1}) \tag{5}$$

where R_s and R_p are the resistances to water flow in the soil and plant, respectively, Ψ_s is the soil water potential, Ψ_1 is the leaf water potential, and T is transpiration or water flux rate through the system.

The results presented in Figures 21 and 22 show the relationship of liquid phase water transfer resistance to flux rate. This non-Darcy response phenomena of decreasing $R_s + R_p$ with increasing water flux rate has been noted for other species as well (e.g., Stoker and Weatherley, 1971; Boyer, 1974). At a flux rate of 1000 mg $H_2O\cdot dm^{-2}\cdot hr^{-1}$ the $R_s + R_p$ resistances were approximately 5.0, 4.5, 7.5, and 1.5 x 10^6 bar$\cdot$sec$\cdot$cm^{-1} for Dupontia, Carex, Deschampsia, and Geum, respectively. Thus, Geum was able to maintain a lower $R_s + R_p$ than the other species. This may be due to higher root permeability, a higher rooting density, or a larger root surface area. Although Geum has a tap root system unlike the fibrous root systems of the other species, rooting depth was not a factor since all the species were restricted in pots of the same size. However, in the field the ability of Geum to extend its root system to more than a meter in depth may be an important advantage in utilizing water at greater depths.

Since it is well established that decrease in guard cell turgor causes the stomatal pore to occlude (e.g., Slatyer, 1967; Kozlowski, 1972), another mechanism which may be responsible for relatively low r_s in the wider ranging species at low Ψ_s may be a stomatal mechanism which is not as sensitive to turgor pressure decline as

Figure 21. Liquid phase water transfer resistances ($R_s + R_p$) for *Dupontia fischeri* and *Carex aquatilis* determined at a leaf temperature of 20°C, 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated, and at varying soil moisture levels. Visual regression estimates have been drawn in to fit the individual data points.

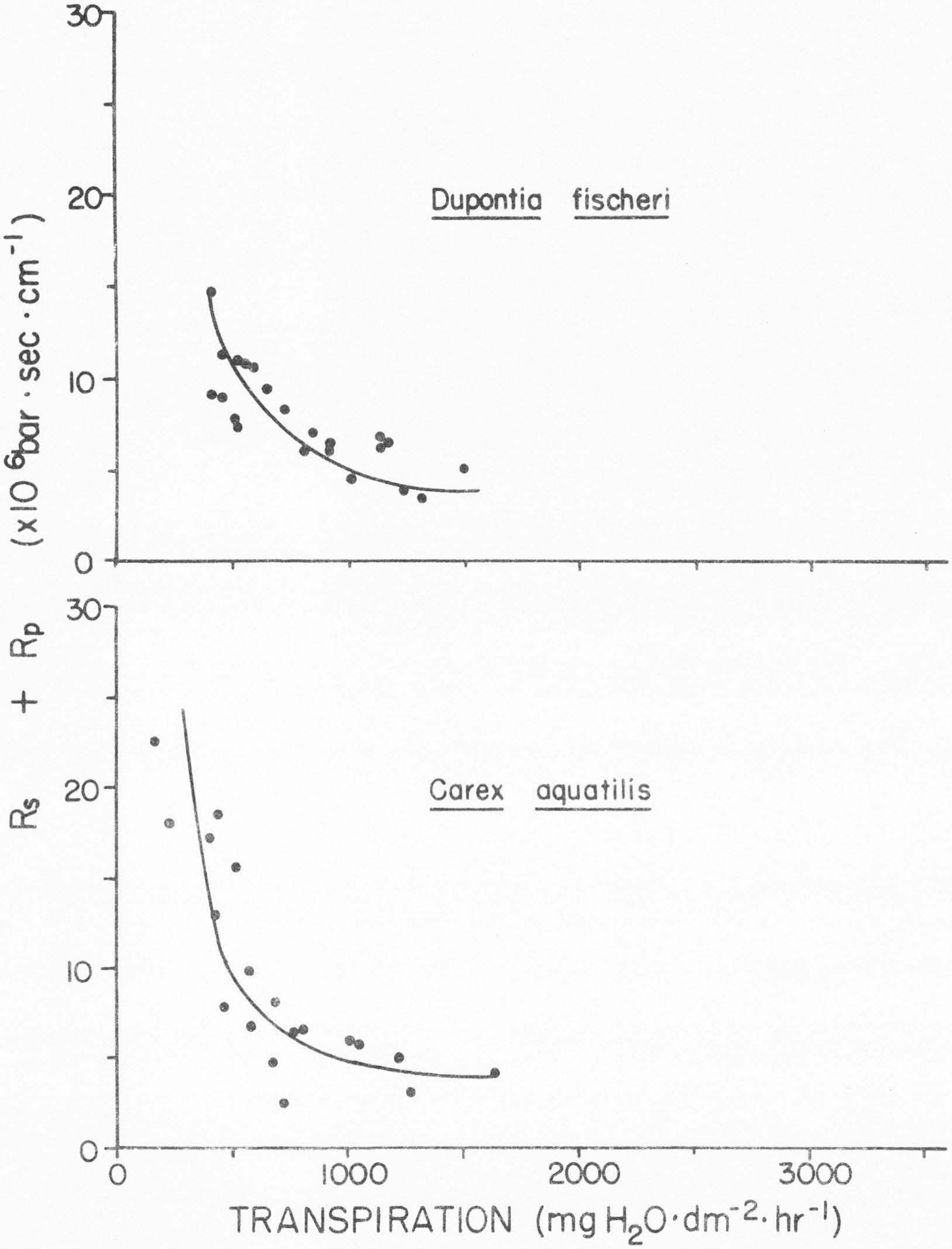
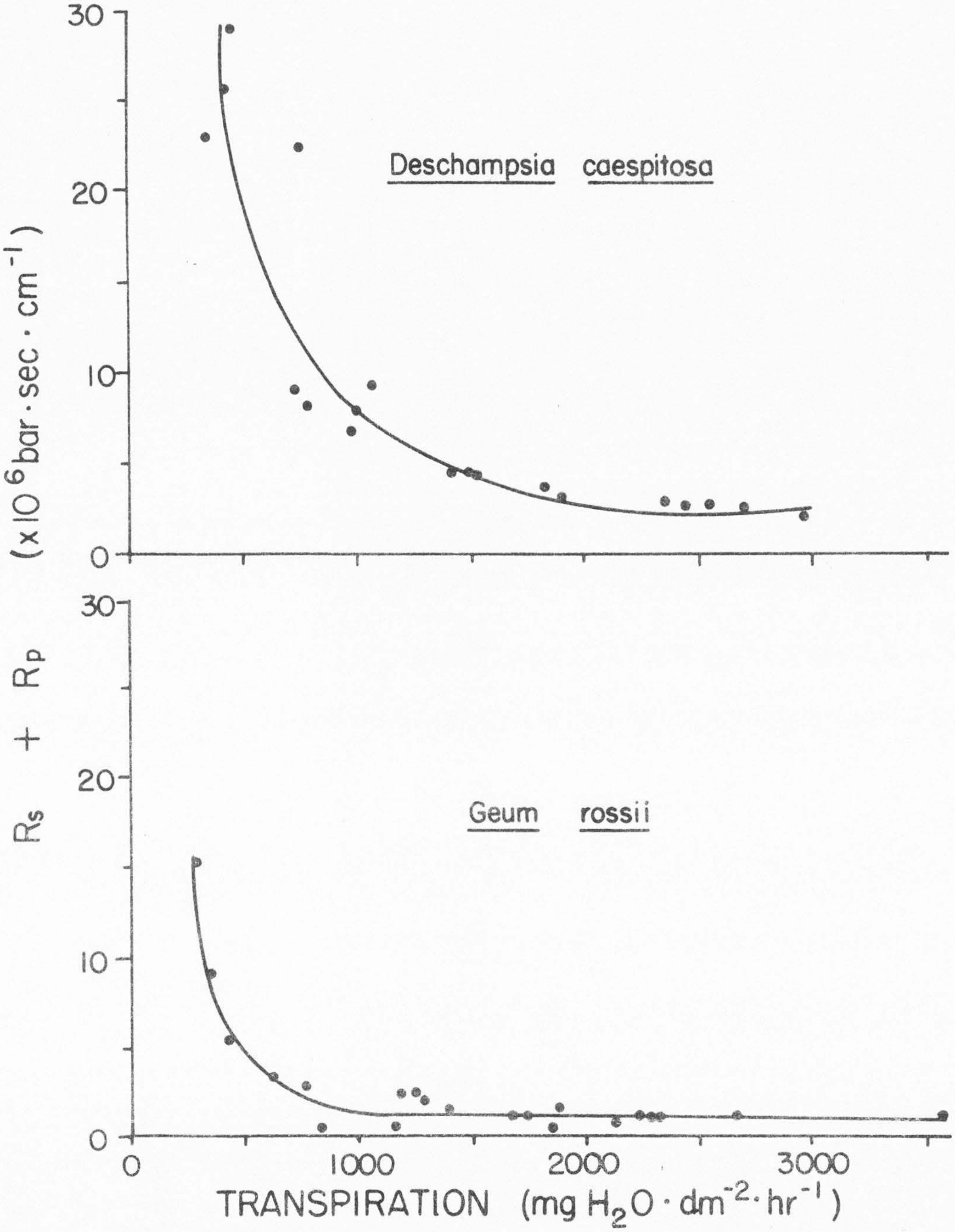

Dupontia fischeri
Carex aquatilis
$R_s + R_p$ (x10^6 bar · sec · cm^{-1})
0
10
20
30
0
1000
2000
3000
TRANSPIRATION (mg H_2O·dm^{-2}·hr^{-1})

Figure 22. Liquid phase water transfer resistances ($R_s + R_p$) for Deschampsia caespitosa and Geum rossii determined at a leaf temperature of 20°C, 900 $\mu e \cdot m^{-2} \cdot sec^{-1}$ (400-700 nm) where photosynthesis was light-saturated, and at varying soil moisture levels. Visual regression estimates have been drawn in to fit the individual data points.


30
20
10
0
30
20
10
0
1000
2000
3000
Deschampsia caespitosa
Geum rossii
$R_s + R_p$ $(\times 10^6 \mathrm{bar \cdot sec \cdot cm^{-1}})$
TRANSPIRATION $(\mathrm{mg\ H_2O \cdot dm^{-2} \cdot hr^{-1}})$

compared with species restricted to wet tundra habitats. In order to examine this possibility, the pressure potential component, Ψ_p, was determined for each tundra species over a range of moisture stress conditions. Since Ψ_p as measured in this study represents an integrated measure of the different cells in the entire leaf sample, Ψ_p should be reasonably indicative of changes in guard cell turgor.

Figures 23 and 24 show the relationship of Ψ_p and Ψ_l in the four tundra species. The range of Ψ_l values in this study represent values which these tundra species may experience in the field. As shown in Chapter III, Ψ_l reached -30 bars in Deschampsia and -20 bars in Geum on Niwot Ridge in Colorado during the 1972 field season. At Barrow, Alaska, during the 1973 field season Ψ_l of -13 bars and -15 bars for Dupontia and Carex were measured, respectively (Stoner and Miller, unpublished data). Figures 23 and 24 suggest that apparently negative Ψ_p develop in all four species. A number of authors have also reported negative Ψ_p (Kreeb, 1963; Noy-Meir and Ginzburg, 1969; Warren Wilson, 1967; Brown, 1972). However, Slatyer (1967) suggests that negative Ψ_p may be merely due to technique artifacts. These artifacts may be the result of matric forces if the measurement technique includes certain matric forces in estimates of water potential for living tissue, but excludes them for killed tissue or may involve changes in the average Ψ_π due to mixing of the solutions from the various phases, varying in composition and concentration, when the leaf is killed (Noy-Meir and Ginzburg, 1967). Whether or not the negative Ψ_p found in this

Figure 23. Ψ_p and Ψ_1 regressions with individual data points for *Dupontia fischeri* and *Carex aquatilis* with r values of .92 and .84, respectively. The regressions for both *Dupontia* and *Carex* are statistically significant at the .99 level but do not statistically differ from each other.

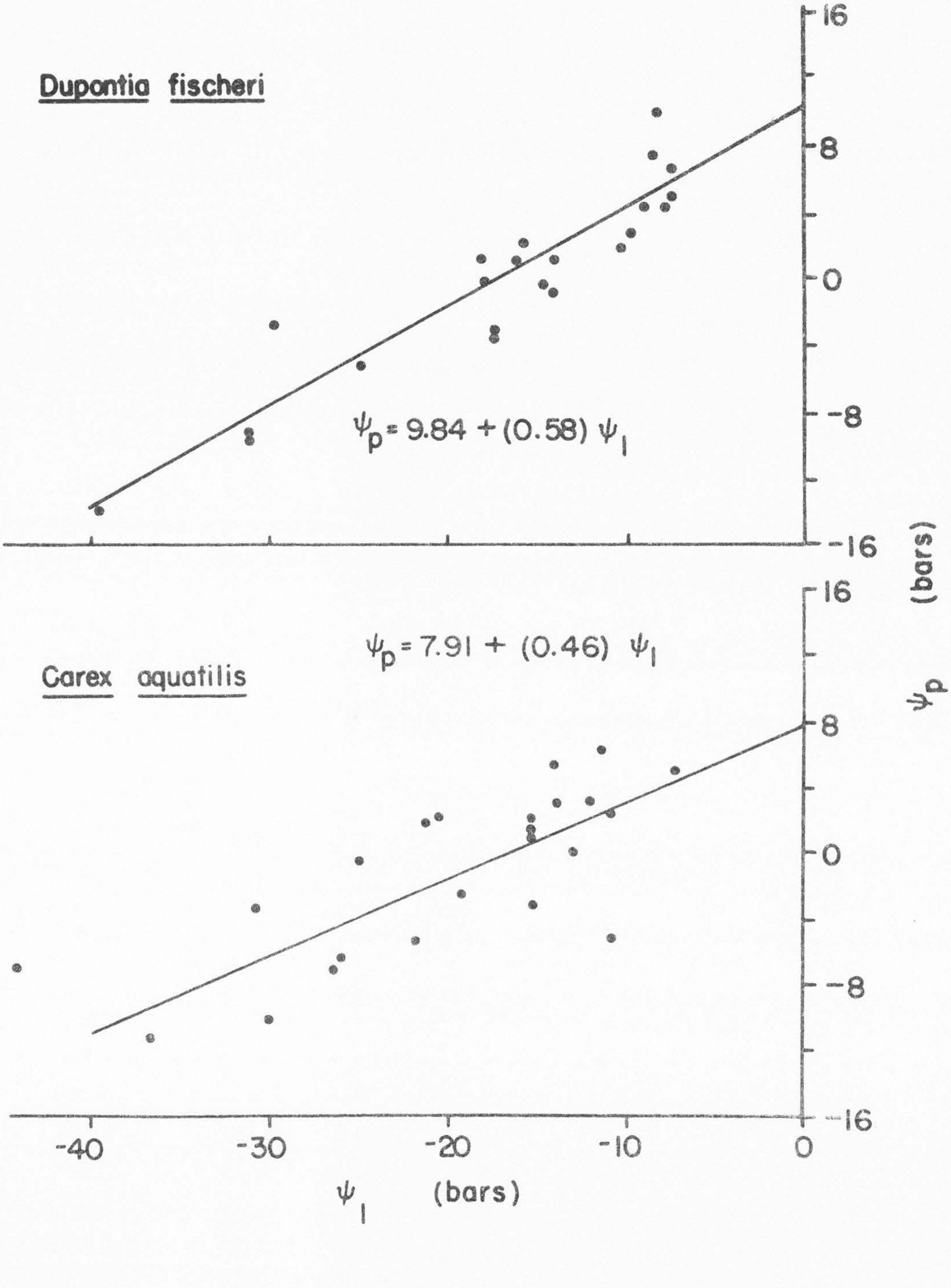
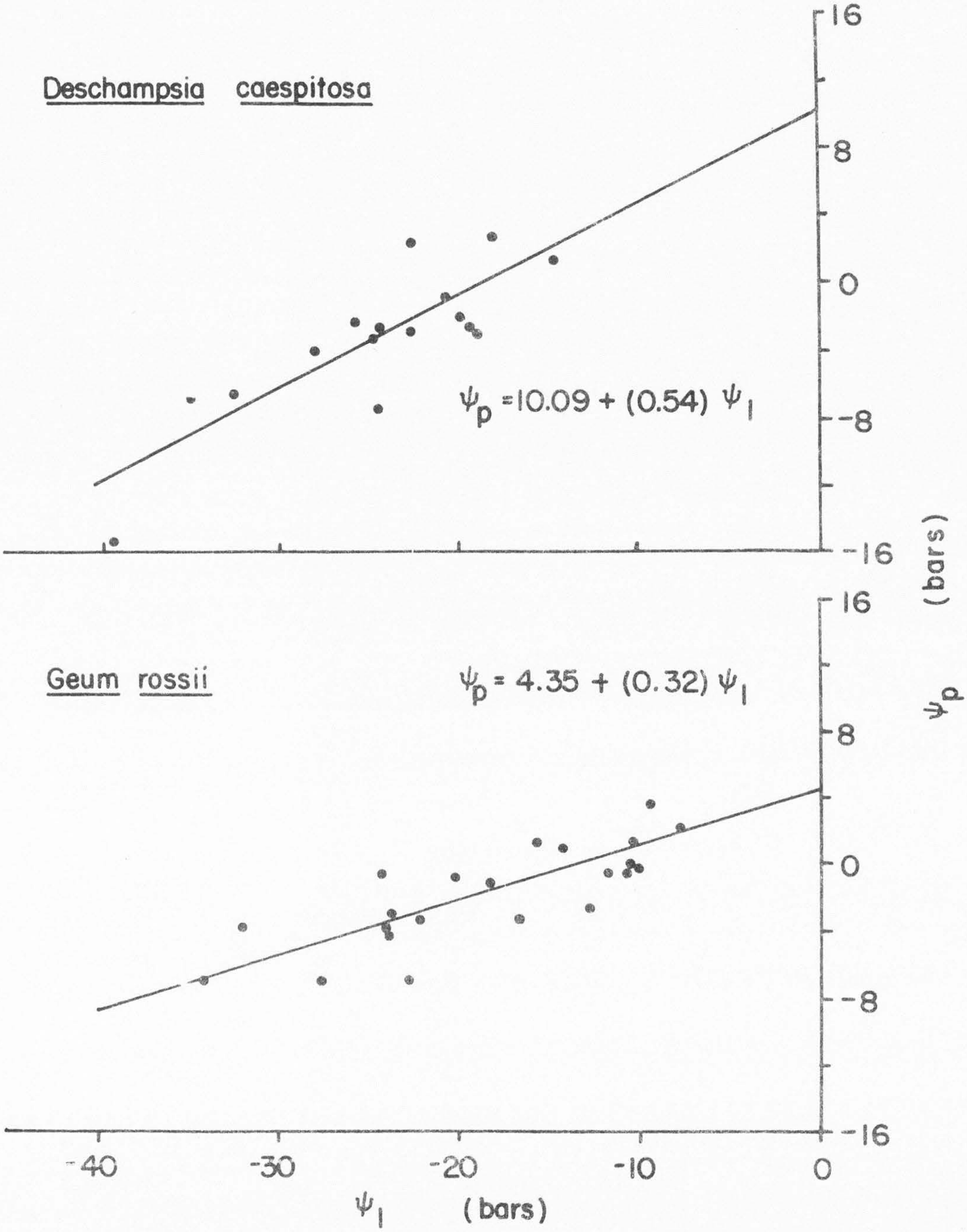

Dupontia fischeri
$\psi_p = 9.84 + (0.58)\ \psi_l$
Carex aquatilis
$\psi_p = 7.91 + (0.46)\ \psi_l$
16
8
0
-8
-16
ψ_p (bars)
-40
-30
-20
-10
0
ψ_l (bars)

Figure 24. Ψ_p and Ψ_l regressions with individual data points for Deschampsia caespitosa and Geum rossii with r values of .83 and .80, respectively. The regressions for both Deschampsia and Geum are statistically significant at the .99 level and also are statistically different from each other at the .99 level.


Deschampsia caespitosa
$\psi_p = 10.09 + (0.54)\ \psi_l$
Geum rossii
$\psi_p = 4.35 + (0.32)\ \psi_l$
16
8
0
-8
-16
16
8
0
-8
-16
ψ_p (bars)
-40
-30
-20
-10
0
ψ_l (bars)

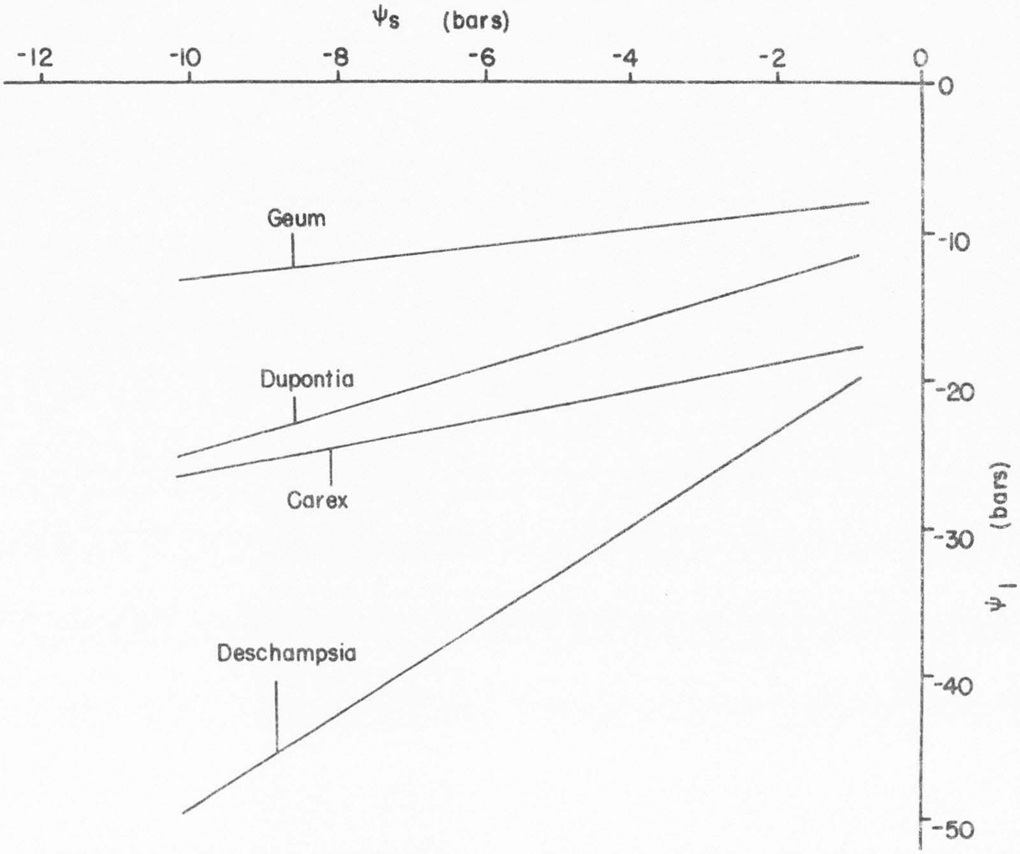
study indeed are technique artifacts, the results between the wet site and wider ranging species should be reasonably comparable on a relative basis.

Deschampsia, an alpine tundra species restricted mainly to wet meadow habitats, exhibited a significantly different Ψ_p and Ψ_l relationship than Geum, the wider ranging alpine tundra species. A similar trend is suggested in the arctic tundra species; however, because of the wider variability in data points for these species, their Ψ_l and Ψ_p slopes are not statistically different. Alternatively, this lack of significance may reflect the smaller differences in magnitude between the arctic tundra habitats where Dupontia and Carex are found.

For the alpine tundra species and possibly for the arctic tundra species, a decline in Ψ_l would produce a larger decline in Ψ_p in species restricted to wet meadow areas than in broader ranging species. These data also suggest that the wet site species may exhibit larger Ψ_p at high Ψ_l. In addition Ψ_l and Ψ_s relationships (Figure 25) show that Deschampsia has a statistically significant steeper decline in Ψ_l with decreasing Ψ_s than Geum. These results combined with the Ψ_p and Ψ_l relationships suggest that for the alpine species and possibly for the arctic species a decrease in Ψ_s would produce a larger decline in Ψ_p in the wet site species than in the wider ranging species.

If the Ψ_p measurements in this study truly reflect stomatal turgor behavior, this may be one mechanism which may explain the maintenance of lower r_s in Geum as compared with Deschampsia

Figure 25. Ψ_1 and Ψ_s regressions for Geum rossii, Dupontia fischeri, Carex aquatilis, and Deschampsia caespitosa with r values of .83, .98, .93 and .84, respectively. All regressions are statistically significant at the .99 level. The regression for Geum is statistically different from Deschampsia at the .99 level. The other species regressions do not statistically differ from each other. The number of observations for each regression ranged from 16 to 20.


ψs (bars)
-12
-10
-8
-6
-4
-2
0
0
-10
-20
-30
-40
-50
ψl (bars)
Geum
Dupontia
Carex
Deschampsia

and possibly also for Carex as compared with Dupontia. As moisture stress increases, Deschampsia and possibly Dupontia would experience larger declines in Ψ_p than the wider ranging species and would result in a larger degree of stomatal occlusion in these wet site species.

Since it is generally agreed that growth rate is promoted by an increase in turgor (e.g., Cleland, 1971; Ray, Green, and Cleland, 1972), the wet site species besides exhibiting earlier stomatal closure would likely show earlier declines in their growth rates than the wider ranging species with decreasing Ψ_s. This trend may be offset by the ability of the wet site species to maintain a higher Ψ_p and hence a higher growth rate than the wider ranging species at high Ψ_s. As a result, at high Ψ_s the wet site species would likely exhibit a higher growth rate than the wider ranging species. However, with decreases in Ψ_s the wet site species may exhibit larger declines in Ψ_p and consequently growth rate than the wider ranging species. The field results of Johnson and Caldwell (1974) working with the same two alpine tundra species suggest that at high Ψ_s the wet site species, Deschampsia, exhibited higher leaf relative growth rates than the wider ranging species, Geum.

Differences in the relationship between turgor pressure and water stess have been noted by a number of authors (e.g., Wadleigh and Gauch, 1948; Brown, 1975). These differences in turgor pressure response may be associated with differences in cell wall elasticity which have been determined for a number of species

(Warren Wilson, 1967; Noy-Meir and Ginzburg, 1969; Tyree and Hammel, 1972). These differences in cell wall elasticity may likely affect the amount of change in turgor pressure for a given change in leaf hydration. As a result, for a given amount of water loss from a turgid cell, an elastic cell would tend to decrease in volume and thereby maintain turgor within the cell. In contrast a rigid, inelastic cell would tend to retain the same volume, and thus, would experience a relatively greater reduction in turgor.

Cell wall elasticity, e, or coefficient of enlargement as Broyer (1952) prefers, can be calculated using the following equation derived by Warren Wilson (1967b):

$$e = \frac{(\Psi_{\pi_t} + \Psi_{m_t}) - [(\Psi_{\pi_t} + \Psi_{m_t}) + \Psi_p]}{1 - R} \quad \text{(bars)} \qquad (6)$$

where $(\Psi_{\pi_t} + \Psi_{m_t})$ is the combined osmotic and matric potential component at full leaf turgor and Ψ_p and R represent the pressure potential component and the relative leaf water content at some leaf hydration less than full turgor, respectively.

Assuming that the matric potential component in plants is negligible compared to the osmotic potential component (Wiebe, 1966) and that the osmotic potential component is directly proportional to the solute concentration (Gardner and Ehlig, 1965):

$$R = \frac{(\Psi_{\pi_t} + \Psi_{m_t})}{(\Psi_\pi + \Psi_m)} \qquad (7)$$

where $(\Psi_\pi + \Psi_m)$ is the combined osmotic and matric potential component at some leaf hydration less than full turgor. Then, substituting in equation 6:

$$e = \frac{(\Psi_{\pi_t} + \Psi_{m_t}) - [(\Psi_{\pi_t} + \Psi_{m_t}) + \Psi_p]}{1 - \frac{(\Psi_{\pi_t} + \Psi_{m_t})}{(\Psi_\pi - \Psi_m)}} \quad \text{(bars)} \qquad (8)$$

As Noy-Meir and Ginzburg (1967) discuss, equations similar to equation 8 assume that plant tissue is a single phase of dilute ideal solution, enclosed by elastic wall which are either very thin or have no affinity to water. Furthermore, they point out that these assumptions may not hold true for highly complex and heterogenous leaf tissues because of their non-ideal solute behavior, non-linearity of leaf turgor with leaf water content, and possibly appreciable matric potentials. However, after considerable theoretical consideration, Noy-Meir and Ginzburg (1967) conclude that even though all of the above assumptions may not be entirely correct, present methods of partitioning water potential components of leaf tissue can still be considered as a first approximation.

Table 2 shows cell wall elasticity, e, as calculated from equation 8 for the four tundra species. Values for the parameters used in calculation of e were taken from regressions of Ψ_1, Ψ_π, and Ψ_p and are also listed in Table 2. High values of e reflect a relatively rigid, inelastic cell wall, whereas small e indicate a somewhat elastic cell wall. These calculations suggest that Geum and Carex, the wider ranging species, have more elastic cell walls as compared with the rather rigid, inelastic cell walls in the wet site tundra species, Deschampsia and Dupontia. As a result, for a given amount of water loss from a turgid cell, an elastic cell as suggested for the wider ranging species would tend to decrease in volume and thereby maintain Ψ_p within the cell. In contrast, a rigid, inelastic cell wall as suggested for the wet site species would tend to retain the same volume and thus would experience a relatively greater reduction in Ψ_p.

Table 2. Cell wall elasticity, e, for Deschampsia caespitosa, Geum rossii, Dupontia fischeri, and Carex aquatilis. The values for the parameters used in calculating e were taken from regressions of Ψ_l, Ψ_π, and Ψ_p.

Species	$\Psi_{\pi_t} + \Psi_{m_t}$ (bars)	Ψ_p (bars)	$\Psi_\pi + \Psi_m$ (bars)	e (bars)
Deschampsia	-13.4	4.7	-14.7	52
Geum	- 9.5	1.2	-11.2	8
Dupontia	-12.9	4.0	-14.0	50
Carex	-11.8	3.8	-13.8	27

Cell wall elasticity may have a regulatory effect of partitioning declines in Ψ_l between Ψ_p and Ψ_π as suggested by Noy-Meir and Ginzburg (1969). They suggest that this mechanism may be an attribute if it diverts most of the drop in Ψ_l to that component which damages the plant the least. For example, the relatively elastic cell walls suggested for the wider ranging species, Geum and Carex, produce a rather small reduction in Ψ_p and necessarily produce a larger reduction in Ψ_π. As a result, Geum and Carex may be more sensitive to declines in Ψ_p than to increasing solute concentration. In contrast, the rather rigid, inelastic cell walls suggested for Deschampsia and Dupontia would result in a steeper decline in Ψ_p than compared to Ψ_π and consequently may be more sensitive to declines of Ψ_π than to reductions of Ψ_p.

The results of this study show that tundra plants have differential attributes with respect to moisture stress and suggest that these attributes may be important contributing factors in determining the local distribution of these species. However, it must be emphasized that on a long term survival basis these attributes may be tempered or even masked by the vast array of other biotic and abiotic factors which constitute the environmental complex of the plant.

CHAPTER VI

CONCLUSIONS

1. Although not all habitats within the alpine tundra area of Niwot Ridge in Colorado are constantly under moisture stress, moisture stress may develop in at least the more exposed fellfield sites.
2. The photosynthetic capacity of *Deschampsia caespitosa* and *Dupontia fischeri*, tundra species restricted mainly to wet meadow areas, were higher under conditions of low moisture stress than those of the more widely distributed tundra species, *Geum rossii* and *Carex aquatilis*.
3. The wider ranging tundra species were able to maintain greater photosynthetic capacity as soil moisture stress increased than the species typically restricted to wet meadow areas.
4. Although the depression of net photosynthesis with water stress in these four tundra species was partially attributed to reduced stomatal aperture, with decreased soil water potential most of the decline in photosynthesis was due to a greater non-stomatal or residual resistance, indicating a direct impact of water stress on the photosynthetic apparatus.
5. Although photorespiration may have increased with enhanced water stress, greater mitochondrial respiration is unlikely involved in the depression of photosynthesis in these four tundra species.

6. The species mainly restricted to wet meadow tundra areas typically exhibited higher photosynthesis/transpiration ratios than species having a wider ranging microsite distribution at high soil water potentials; however, as soil water potentials decreased, the more widely distributed tundra species generally maintained higher photosynthesis/transpiration ratios.
7. At high soil water potentials stomata of the species restricted typically to wet meadow tundra areas did not appear to undergo a closing response until the bulk leaf water potential decreased; however, reduced stomatal aperture of the tundra species with a wider distribution was noted before leaf water potential dropped.
8. Although the stomatal mechanism of the tundra species restricted typically to wet meadow areas exhibited lower degrees of stomatal occlusion than the wider distributed tundra species at high soil water potentials, the wider ranging species exhibited lower levels of stomatal occlusion than the species restricted to wet meadow areas as soil water potential decreased.
9. *Geum rossii* was able to maintain a lower liquid phase water transfer resistance from the soil to the leaf than the other tundra species.
10. As moisture stress increased, *Deschampsia caespitosa* experienced a larger decline in bulk leaf turgor pressure than *Geum rossii*.
11. Calculations of cell wall elasticity indicated that the wider ranging tundra species have more elastic cell walls as compared

with the relatively more inelastic cell walls in the species restricted to wet meadow tundra areas.

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