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thesis entitled

THE WATER RELATIONS OF TWO SPECIES OF CO-OCCURRING GOLDENRODS (Solidago)

presented by

Martha Ann Potvin

has been accepted towards fulfillment of the requirements for

Master degree in Botany

Patricia A. Werner

Major professor

Date 30 July 1980

THE WATER RELATIONS OF TWO SPECIES OF CO-OCCURRING GOLDENRODS (Solidago)

by

Martha Ann Potvin

A THESIS

Submitted to
Michigan State University
in partial fulfillment of the requirements
for the degree of

MASTER OF SCIENCE

Department of Botany and Plant Pathology

1980

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ABSTRACT

THE WATER RELATIONS OF TWO SPECIES OF CO-OCCURRING GOLDENRODS (*Solidago*)

By

Martha Ann Potvin

Field, greenhouse, and laboratory experiments were conducted to determine the water relations of two co-occurring species of goldenrods, *Solidago canadensis* L. (usually found on moist sites) and *S. juncea* Ait. (usually found on dry sites).

In the field, both species reached leaf water potentials of <-20 bars without stomatal closure. Greenhouse measurements of stomatal conductances and leaf water potentials on transplants and seedlings grown accross an experimental soil moisture gradient indicate a lack of differences in species' response to different soil moisture levels. *S. juncea* seedling leaf water potentials were lower than those of *S. canadensis*. *Solidago juncea* had a higher adaxial/abaxial stomatal ratio than *S. canadensis*. Gas analysis determinations of assimilation rates, stomatal conductances and water use efficiencies indicated that both species have similar water use physiologies.

Differences in physiology, morphology, phenology and life histories are discussed as factors causing the differential distributions and competitive abilities of the two species.

To my parents: I am indebted

to them for years of support and

encouragement.

ACKNOWLEDGEMENTS

I am especially thankful to my major professor, P. A. Werner for her support and valuable comments on this thesis. She provided me with lab space and equipment for the project as well as with the technical assistance of J. H. Grace, A. M. Bair ad K. M. Wiest.

I am indebted to Dr. S. N. Stephenson who provided me with the opportunity to come to MSU, office space, many stimulating discussions, advice, and helpful comments on this thesis. I also wish to thank Dr. G. Safir for stimulating my interest in plant water relations, and for providing technical advice and useful comments on my thesis.

This research would have been impossible without assistance, equipment, or funds provided by the following: Dr. G. H. Lauff, who provided me with facilities and teaching assistantships at KBS, the KBS secretaries, especially S. Wickham who helped in the final preparation of this thesis, the MSU Department of Botany for providing me with teaching assistantships and funds to perform the computer analysis of my transplant data, the DOE at MSU for the use of their growth chamber, IR gas analyzer and a microscope, Dr. J. L. Lockwood for the use of the ceramic pressure plate apparatus, Dr. M. Pierce and M. Mispagel who lent me pressure bombs, Dr. R. Wetzel for the use of a Coleman lamp, A. Winn for assistance on one of the sampling dates and in the excavation of the source clones, Dr. C. Cress for statistical advice, J. H. Grace for maintaining my plants in the greenhouse and the preparation of figures.

I am especially thankful to T. Sharkey who taught me how to operate, maintain and interpret data from the IR gas analyzer.

Many people helped me tremendously with their friendship, understanding and indirect support of my research. Among them are my family, B. Hutchinson, F. Fish, H. W. Deckelbaum, C. Doner, M. Kohring, S. Weiss, J. Kelly, C. Carmichael, J. Bopry, K. Gross, and R. Gross.

This research was partially funded by NSF grants to P. A. Werner, DEB 7601602 AOI and DEB 7923945.

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INTRODUCTION

The physiological limits of tolerance for organisms are often broader than their ecological distributions indicate. Competition for limited resources may restrict the potential distributions of organisms.

Experimental studies by Connell (1961) with barnacles on rocky intertidal areas, by Ungar et. al. (1969) with halophytes in saline habitats, by Sharitz and McCormick (1973) with annual plants on granite outcroppings, and by Werner and Platt (1976) with goldenrods on soil moisture gradients have dealt with complex gradients which characteristically have one end where abiotic stresses are the greatest and the other end where there is low abiotic stress. The part of the gradient where abiotic stress is the lowest is also the part where biotic interactions are the greatest. The organisms which have their maximum abundances on the end of the gradient characterized by low abiotic stress and a high potential for biotic interactions have relatively fast individual growth rates and high competitive ability. Organisms associated with the abiotically stressed end are characterized by having slower growth rates and physiological and morphological adaptations to deal with the particular "stress" at that end of the gradient. In all of these examples, the organism which was adapted to tolerate abiotic stress had the widest physiological range of tolerance and hence, the potential for the broader distribution, yet it was competitively excluded from the more optimal (in terms of growth and

reproductive potential) habitat, that which was occupied by the organism with the higher competitive ability.

It is possible that the maintenance of such adaptations for coping with environmental extremes is balanced by a decrease in growth rate and in competitive ability when compared with a species which is specialized in exploiting the less variable portions of that resource.

In the previous examples, the particular morphological and physiological mechanisms or adaptations which allow one species to be designated as a better competitor or which allow it to tolerate stress have been inferred, but not well studied.

A mechanistic approach has been taken by Pickett and Bazzaz (1976, 1978a) who, in greenhouse experiments, studied the physiological response of annual plants when grown alone on a gradient of depth-to-water-table and then made and tested predictions as to what their distributions would be when growth together. They recently compared the competitive abilities with the water use physiologies of these annual species (Pickett and Bazzaz 1978b). The water use patterns explain a few, but not all of the distributional patterns and competitive abilities of these species.

There are a few recent ecological studies which have applied modern methods and advances from physiological studies of water use patterns of crop plants to studies which attempt to explain the distributions of species in nature; these have dealt mainly with adaptations for survival in desert or alpine habitats or in resource partitioning by unrelated co-occurring taxa (see Mooney 1976, for a review). Physiological mechanisms of competition based on water use strategies of closely related co-occurring species have received little attention. This study

is an attempt to identify some of the physiological mechanisms which contribute to the differential distributions and competitive abilities along soil moisture gradients of two species of goldenrods (Solidago) by studying their water relations.

Werner and Platt (1976) showed that the same five species of goldenrods co-occurred in an Iowa virgin prairie and a Michigan old field with the same ranking along comparable soil moisture gradients. Interspecific competition has been suggested as a possible explanation of these distributional patterns.

Using two of these species, Werner has experimentally demonstrated in the field with reciprocal transplants, and in the greenhouse with seedlings, that species from both dry and wet ends of the gradient grow best (in terms of size and survival) on the moister sites. Solidago juncea, the dry end species not only survived on dry sites with and without competitors, but grew largest on moister sites when grown alone. It grew poorly on moister sites in the presence of competitors. Solidago canadensis, the wet site species, grew best on moister sites with or without competitors and grew poorly or not at all on dry sites whether or not competitors were present (Werner, unpublished data).

On moist sites, S. canadensis seemed to have a competitive advantage by maximizing growth rate and S. juncea was displaced to drier areas where S. canadensis could not compete due to water limitations. The persistence of S. juncea at the dry end of the gradients could be due to physiological or morphological adaptations to tolerate the abiotically stressful conditions there. For S. juncea, there may be a tradeoff between the benefits of maintaining adaptations allowing survival under conditions of decreased water availability and the

benefits of rapid growth rates. This would account for the wider potential distribution but decreased competitive ability of S. juncea compared to S. canadensis at the wet end of the gradient (Werner unpublished).

There are many and complex physiological responses to water stress. The earliest responses include decreased cell expansion and stomatal closure.

Stomata are the major sites of gas exchange and water loss from the plant. Their movement is sensitive to leaf water status. Stomatal regulation is the major plant mechanism for controlling water loss from leaves when soil water is in short supply. Measurements of stomatal conductances to water vapor have been used to determine the levels of water stress in crop plants.

When stomata are open and transpiration occurs, the concentration of solutes in the mesophyll cells increases, as does the xylem (-) pressure potential, causing a water potential gradient between the leaves and the roots which is the driving force for water movement through the plant. The water potential gradient or driving force pulling water up to the leaves is relatively easily measured and is often used in analyses of plant water relations (Boyer 1969, Hsiao 1973, Ritchie and Hinckley 1975).

If high stomatal conductances are accompanied by high transpiration rates, plant water potential will decrease if the roots cannot supply soil water to the leaves at a rate equal to the rate of transpiration. The resulting increase in the cellular concentration of solutes (increased solute potential and decreased turgor) may cause eventual cellular damage. If stomatal closure occurs when evaporational demands

are high, transpiration, photosynthesis, and growth will cease. Stomatal closure early in the day may result in high leaf temperatures due to a lack of evaporative cooling and may injure the plant. Not all stomatal closure is detrimental to the plant; nightime closure of stomata can prevent unnecessary water loss. There must be balanced short term (diurnal) and long term (seasonal) regulation of stomata so that plants can survive changing moisture conditions.

Differences in the water use patterns of S. canadensis and S. juncea and their response to water stress could, in part, account for their characteristic distributions and their differential competitive abilities. The parameters which may have ecological consequences and which were considered in this study were seasonal and diurnal differences in stomatal conductances and leaf water potentials, and stomatal distributions at various growth stages as well as conductances, assimilation rates, and water use efficiencies in response to a range of light intensities.

The comparative approach of this study involved three phases: 1) In situ field measurements of leaf conductances to water vapor and leaf water potentials during the course of a day, 2) Greenhouse measurements of stomatal conductance, water potentials and stomatal distributions made during the summer on transplants and seedlings grown on an experimental soil moisture gradient and 3) Laboratory studies to assess stomatal conductances, assimilation rates, and water use efficiencies under different light intensities.

CHAPTER I. IN SITU STUDIES

METHODS

Solidago juncea Ait. (Early goldenrod) is a native, rhizomatous perennial herb which usually occurs on dry, open sites. Most of the ramets are broad leaved vegetative rosettes with leaves which are elevated from the ground. Flowering stems, have determinate inflorescences with leaves decreasing rapidly in size upward, and a height of 0.1-0.4 m. Deep roots arise from the rhizome.

Solidago canadensis L. (Canada goldenrod) is a native, rhizomatous, herbaceous, perennial which occurs commonly throughout the U. S. and Canada in dry and moist fields and in forest openings. Most of the ramets produce flowers in a determinate inflorescence in a given year. Leaves are numerous and crowded along the stem which is 0.3-1.5 m in height. Deep roots arise from the rhizomes. (See Werner et. al. 1980, for a recent review of this species).

S. juncea flowers earlier than S. canadensis. In 1979, in the area studied, S. juncea flowered in late August and S. canadensis in late September.

Attractive qualities in both species which made them suitable for physiological studies were the perennial habit, the availability of rhizomatous material, and leaves large enough on which to make measurements.

B Avenue Field was chosen as the study site because of its

accessibility to KBS and the author's familiarity with the site. This field is located just to the West of Long Woods, at the corner of B Avenue and East Gull Lake Drive on the Kellogg Biological Station (KBS) property in Kalamazoo County, Michigan (R9W, Sec. 8, NW1/4). The field, abandoned from cultivation in 1964, supports a mixture of forbs, grasses, shrubs, and saplings including six species of Solidago. Clones of S. juncea and S. canadensis (variety scabra) were abundant in this field.

In April, 1979, for each of the two species, three clones from two relatively dry sites and three clones from two relatively wet sites were chosen. The wet and dry sites were chosen on the basis of the topography of the field. The lowest area was selected as the wettest site (field site 4). The two driest sites were on a shallow grade (field site 1 was the highest). Voucher specimens were collected from all six clones of each species and were placed in the KBS herbarium.

The soil moisture characteristic curves for the soils from these four fieldsites are presented in Figure 1 (cf. Appendix A). Soil samples were analyzed on a ceramic plate extractor (Soil-moisture Equipment Corp., CA) to obtain these curves. Before the analyses, samples were air dried and passed through a 2.38 mm sieve. For gravimetric determinations, the samples were air dried in a forced air oven for 24 hrs at 100 C.

The similarity of these curves indicates that all four fieldsites have similar soil types, are similar in their water content and are similar in the amount of water which is available for growth as the soil dries. This is especially evident when compared with the experimental gradients used later in this study (Chapter II).

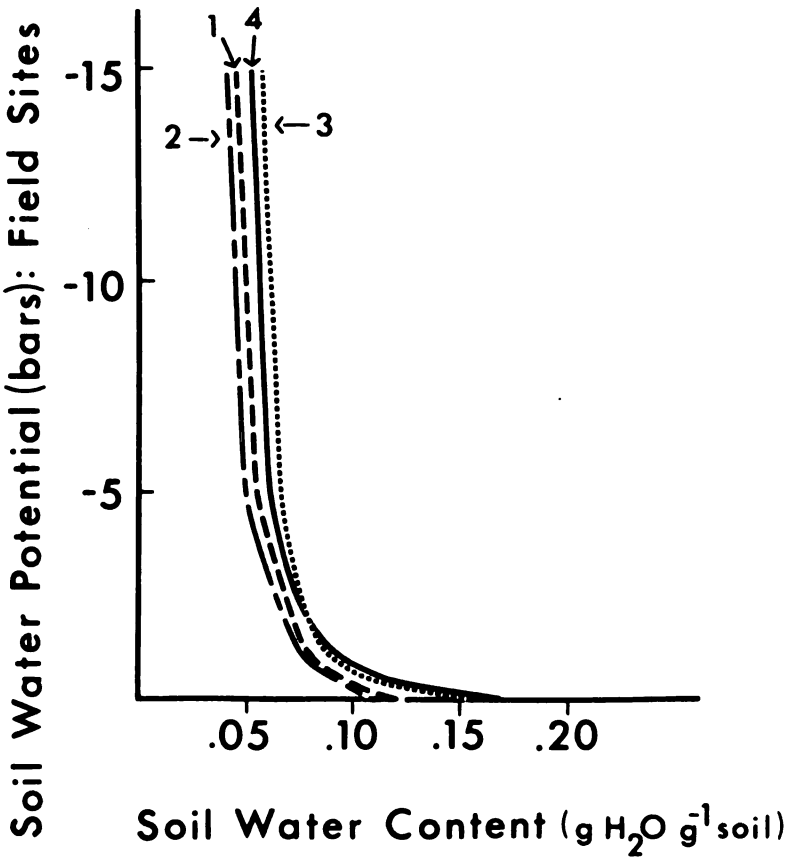

Figure 1. Soil Characteristic Curves: Fieldsites (1 = driest, 4 = wettest)

The seasonal water content of the soils from these four fieldsites are presented in Figure 2 (cf. Appendix B). The amount of soil moisture in the four fieldsites was similar throughout the summer. Actually, the sites chosen as the driest (sites 1 and 2) did not always have the lowest moisture content although site 4 consistently had the highest.

Figure 3 depicts the summer rainfall data collected daily at KBS for the summer of 1979 (cf. Appendix C). It rained on 16 of the 31 days in August and the soil stayed relatively moist throughout the summer. Note that the soil water potential dropped from >-1 bar to <-15 bars from the middle of July to the middle of August (Figs. 1 and 2). The peak in soil moisture in September corresponds to the recharging of the soil water from the August rains.

Diel measurements of stomatal conductances and leaf water potentials in the field were taken on September 6, 1979, a partly to mostly sunny day. Measurements were taken in fieldsite 2, from S. juncea and S. canadensis source clones, which were about 1.5 m apart. Single leaf samples were taken from both a vegetative rosette and a post-flowering adult of S. juncea and from a S. canadensis individual (in flower bud), at each successive sampling throughout the day.

Stomatal conductances were measured with a Lamda Model LI-65 diffusion porometer (Kanemasu et. al., 1969) with a sensor aperture of 70 mm^2. Conductances were calculated as the inverse of the diffusive resistance measurements obtained with the porometer. Adaxial and abaxial leaf conductance values were summed to yield a conductance of a one-sided leaf area. See Meidner and Mansfield (1968) for a history of porometry.

The youngest, fully expanded leaves which were fully exposed to the

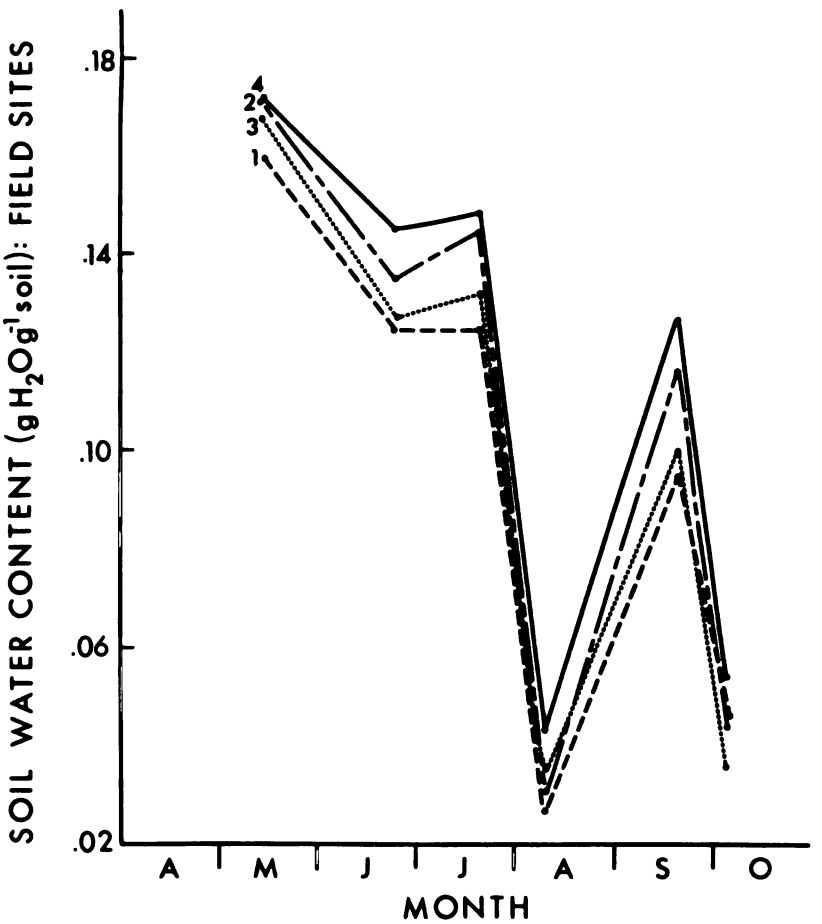

Figure 2. Seasonal Soil Moisture in 1979: Fieldsites (1 = driest, 4 = wettest).

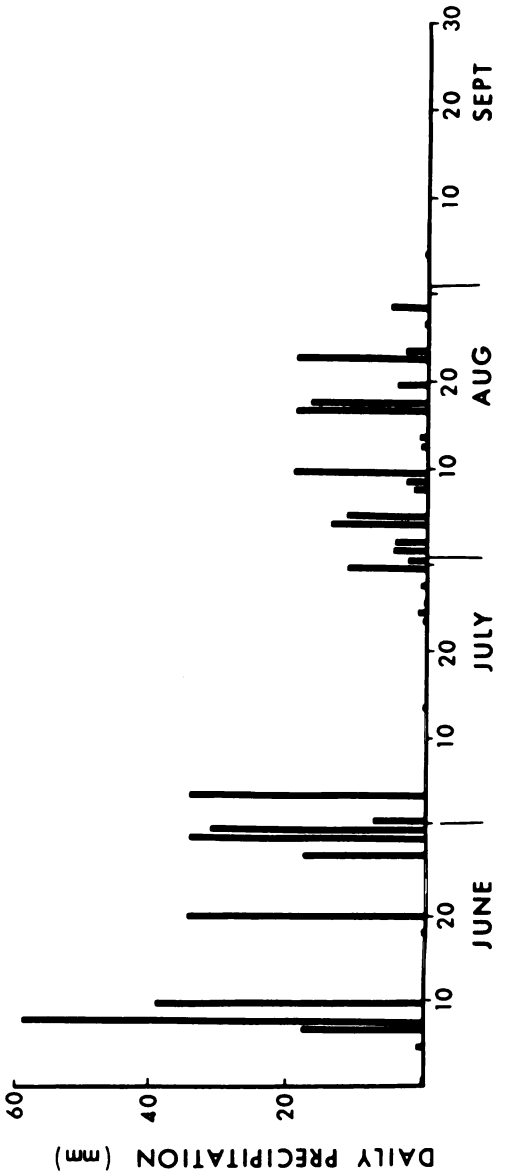

Figure 3. Daily Precipitation During the Summer, 1979.

sun were chosen whenever possible. Sometimes, an older leaf, which was large enough to cover the sensor aperture, had to be selected.

Leaf water potentials were measured with a Scholander-type pressure bomb (Scholander et. al. 1965, Boyer 1969, and Ritchie and Hinckley 1975, for a recent review of theory and applications). Water potential measurements were made on leaves immediately after the conductance measurements were taken.

For leaf water potential measurements, the pressure bomb's rubber stopper (which holds and seals the leaf sample into place in the pressure bomb) was cut in half and the leaf base was placed between the two halves for measurements. During determinations, the pressure was increased at a slow and constant rate. The endpoint was determined when water menisci appeared in 3 major xylem vessels.

In determining water potentials at night, a Coleman lamp was used in the field as a light source, 2-3 m from the clones. Leaves which were covered with dew were blotted with paper towels before the porometer sensor was attached and stomatal conductance measurements were made immediately after blotting.

A one way analysis of variance and a two tailed nonparametric Sign Test (Walker and Lev 1953) were used to test for significant differences between S. canadensis and the two growth stages of S. juncea.

RESULTS

Conductance and water potential measurements from the field diel experiment are presented in Figure 4 (cf. Appendix D). Each data point represents the average of values for two hour intervals.

The S. juncea flowering adults reached significantly lower leaf water potentials than S. canadensis throughout the day (Sign Test,

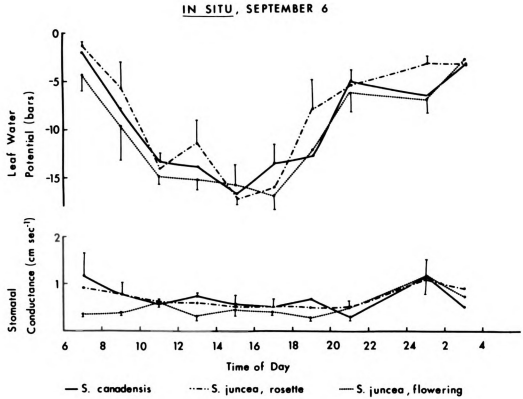

Figure 4. Conductance and Water Potential Measurements: Field Diel, at Fieldsite 2 (dry), September 6, 1979. Data represent means from two hour intervals, vertical bars represent ± 1 S.E.

P=.008). Solidago juncea flowering adults also reached significantly lower water potentials than S. juncea rosettes (Sign Test, P=.004). The Sign Test showed no differences in stomatal conductances of the three groups or in the water potentials of S. juncea rosettes and S. canadensis. The analysis of variance for these data showed no significant differences in conductances or water potentials (Table 1, cf. Appendix E).

The delay in the onset of stress (decreasing leaf water potentials) in the S. juncea rosettes was probably due to the delay in direct sunlight reaching the short rosette leaves. Similarly, the earlier aleviation from stress may be due to their earlier shading.

The low leaf water potential values indicate both the high levels of stress which may occur in the field and the characteristic early afternoon minima. Apparently, judging from the stomatal conductance values, there was no stomatal response to changing light intensities or to the changing water potentials in the leaves. For each species, maximum conductances occurred shortly after midnight.

DISCUSSION

Stomatal opening is usually triggered by light, and once opened, stomata are usually unaffected by leaf water status until a critically low leaf water potential or leaf water content threshold is reached. See Hsiao (1973) for a review of the data on this topic and Meidner and Mansfield (1968) for a general review of stomatal physiology.

For plants which are not water stressed, there are diel cycles in the opening potentials of stomata with maximum opening potentials occurring at midday coinciding with high light levels. Stomata usually close in the dark. Some endogenous opening may occur on a short time

Table 1. Analysis of Variance: Stomatal Conductance, and Leaf Water Potential Measurements, Field Diel, September 6, 1979.

Conductance

source of variance	df	MS	F
treatment	2	0.17	1.41
error	105	0.12	
total	107		

Water Potential

source of variance	df	MS	F
treatment	2	30.5	0.85
error	108	35.8	
total	110		

scale (15-120 min), e.g. Barrs (1971) observed cyclic opening and closing of stomata on water stressed herbaceous plants.

In the experiment reported here, stomatal movement seemed unresponsive to changing light intensities and evaporative demands throughout the day. Even though water potentials as low as -22 bars were recorded in the field, there did not seem to be stomatal regulation of water loss by stomatal closure associated with these low values.

Some species of plants have the ability to osmoregulate, i.e. to alter their cellular osmotic concentrations. By increasing the solute concentrations in their cells, through the synthesis or accumulation of small, osmotically active molecules, plants can maintain full turgor pressure, water uptake from the soil, and growth at low plant water potentials. This decreases the osmotic water potential component of total water potential must be balanced by an increase in the pressure component so that turgidity can be maintained. Because full turgor pressure can be maintained by this mechanism, transpiration and growth rates may remain the same even though leaf water potentials have decreased. These adjustments in osmotic concentrations and turgidity may occur in a few hours in some plants and in others seasonally with increases in drought stress.

In the field study, the lack of stomatal closure at leaf water potentials of -22 bars and the predawn recovery levels of leaf water potentials to about -2 to -5 bars suggests that there may be some osmotic adjustment which prevents the deleterious effects of water stress in S. canadensis and S. juncea.

Dew deposition, although usually restricted to nocturnal periods,

is not continuous throughout the night and may be interspersed with periods of evaporation. The effects of dew deposition on leaves may affect leaf water status directly, by actual entry into the leaves or indirectly, by lowering transpiration rates. The uptake of dew by leaves has been noted in very few plant species and is seldomly adequate to resaturate the leaf (Slatyer 1967). Decreased transpiration rates when dew is present may significantly delay the onset of diurnal water stress.

In the diel study, the higher values of stomatal conductance in the early morning (until 9:00 a.m.) and in the evening (after 9:00 p.m.) corresponded to the times when dew was present on the leaves. The high conductance values obtained at night were most likely due to the presence of dew on the leaves which was not removed by the paper towelling, or, less likely, to short term endogenous rhythms in stomatal opening. These high conductances were also associated with lowered leaf water potentials which suggests some nighttime water loss.

Diurnal patterns in leaf stomatal resistance (1/conductance) and leaf water potentials have been related to water stress by Bacone et. al. (1976) and Ormsbee et. al. (1976) in successional tree species, Ehleringer and Miller (1975) in alpine plants, Halverson and Patten (1974) in desert shrubs, Turner and Begg (1973) and Kanemasu et. al. (1973) in crop plants. Diurnal and seasonal changes in leaf water potentials are correlated with changing evaporational demand and changing soil water potentials. Minimum values of leaf water potentials are reached at midday when evaporative demands are greatest. Recovery from low water potentials is usually greatest just before dawn.

The trend in water potentials in this experiment was consistent with those reported by the previous authors. Maximum water potential values occurred before dawn indicating a recovery from the stress conditions of the previous day. As the sun rose, and with the onset of photosynthesis, the leaf water potential values decreased. Early afternoon minima were reached just after the peak in evaporational demand. Recovery began in the afternoon as the roots were able to supply water to the leaves at a rate faster than it was being lost.

Solidago juncea reproductive stems had recently finished flowering and their leaves had significantly lower leaf water potentials than the rosettes of S. canadensis. Physiological changes during flowering and fruiting or the morphological characteristics of the S. juncea bolting adult may result in lower water potentials than those of the rosettes or of S. canadensis.

The upright stature of the bolting adult increases the distance which water must be transported to reach the leaves compared to the rosette; this increases the internal hydraulic resistance to water flow and could result in lower leaf water potentials. Flowers increase the transpirational surface area of a plant and may be sites of significant water loss. Hormonal changes which occur with flowering and aging could alter biochemical reaction rates, internal plant resistances or the allocation of resources (including water) within the plant. Any of these changes might alter the plant water status enough to result in lower leaf water potentials.

CHAPTER II. GREENHOUSE EXPERIMENTAL GRADIENT STUDIES

METHODS

The soil moisture boxes located in the KBS greenhouse were designed and constructed by Werner in 1977. Each soil moisture box is 0.9 m x 2.7 m x 0.3 m and is divided lengthwise by a solid plywood partition and crosswise by five sections by plywood with the bottom 5 cm open to allow soil water movement between adjacent compartments. Each compartment holds two soil mixture types, creating twelve soil moisture levels in each half of the box. The entire box is lined with heavy plastic. One end of the box is raised 2-3 degrees to fascilitate drainage while the other end has holes in the end wall which allow excess water to drain out.

The soil mixtures were designed to create a gradient of soil moisture holding capacity. The mixtures were various combinations of sand and sandy organic Vita-hume potting soil and were mixed in the following proportions using a standard cement mixer (Werner, personal communication):

Moisture level	Composition by weight
1 (driest)	100% sand
2	90% sand, 10% loam
3	80% sand, 20% loam
4	70% sand, 30% loam
5	60% sand, 40% loam
6	50% sand, 50% loam

Moisture level	Composition by weight
7	40% sand, 60% loam
8	30% sand, 70% loam
9	20% sand, 80% loam
10	10% sand, 90% loam
11 (wettest)	100% loam
12 (same as 11)	

The "driest" soil mixture was put in the upper half of the first compartment and the second "driest" mixture was put in the lower half. The twelfth mixture (at the wettest end) had the same soil mixture as the eleventh. These mixtures simulate the particle size ratios of soils across a soil moisture gradient in a KBS old-field (Werner unpublished). A fine mist sprinkling system positioned 0.5 m above the boxes, insured even watering.

Duplicate samples from each of the eleven resource states were analyzed to determine their soil moisture characteristic curves (for methods, see Chapter I). These data (Figure 5, cf. Appendix F) indicate that both the soil content and the availability of soil moisture (masured as the change in water content as the soil dries) increase as the proportion of sand in the soil decreases.

These data also indicate that the soil moisture levels in the gradient boxes bracket the range of soil moisture levels found in the in situ field study (Chapter I). The field soils have a slightly higher amount of available water as the soil dries than this experimental gradient. This could be due to a higher organic content in the field soils.

In April, 1979, from the periphery of the six clones of each species in the B Avenue Field, three from fieldsites 1 and 2 ("dry") and three from fieldsites 3 and 4 ("wet"), cores of soil and rhizomes were removed with a tulip bulber. After overnight refrigeration,

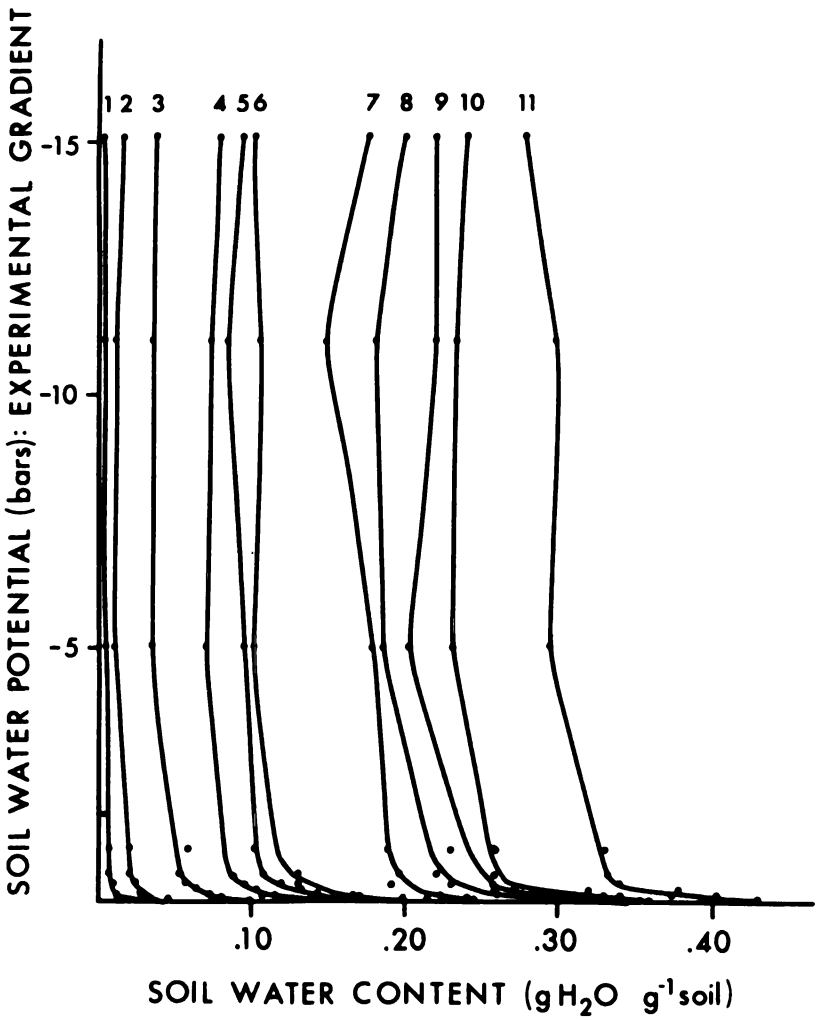

Figure 5. Soil Characteristic Curves: Experimental Gradient Boxes in the Greenhouse (1 = driest, 11 = wettest). Data represent means of two replicates.

uniformly sized young shoots, arising from the rhizomes, were selected and most of the rhizome material at the base was removed. These cuttings were washed, and transplanted into two identical soil moisture boxes in the KBS greenhouse.

Twelve ramets of each genotype (source clone) were transplanted across the gradient, one per level. They were randomly assigned to a position on each of the twelve soil moisture levels and were spaced 11 cm apart such that all 6 genotypes of each species were represented on each soil moisture level. The overall arrangement was in 12 rows of plants across the gradient. If mortality occurred within the first two weeks after transplanting, the dead individuals were removed and replaced with an individual of the same genotype which had been maintained in the greenhouse. The transplants were watered every other day immediately after transplanting to promote rooting and to enhance survival.

Early in May, corresponding to the initiation of seed germination in the field, seeds of each species, collected from the B Ave. Field in the Fall of 1978, were sown into halves of a third soil moisture box in the KBS greenhouse and watered daily until germination was complete. Seedlings were thinned to about 1.5 plants/dm^2.

Commercial Rapid-Gro houseplant fertilizer was applied to the transplants and to the seedlings twice during the summer.

Measurements of stomatal conductances, leaf water potentials and stomatal frequencies were taken at four times during the summer (June 16, June 28, Aug. 2, and Sept. 14) from the transplants. All genotypes from soil moisture levels 3, 6, 9, and 11, representing a broad range across the gradient were selected for these measurements. On each

plant, the youngest, fully expanded leaf, which was large enough to accommodate the porometer sensor was selected for measurement (see Methods, Chapter 1 for conductance and water potential determinations).

The sampling sequence of rows across the gradient was randomized on each of the four sampling dates, but the sequence of sampling within the four levels always proceeded from dry to wet. All measurements were made between 8:00 a.m. and 6:30 p.m. on sunny to partly cloudy days, three to six days after watering.

Stomatal frequencies were determined from replicate peels made with Cutex clear fingernail polish after the leaves were removed from the pressure bomb. The frequencies were calculated for the portion of the leaf which would likely have been covered by the porometer sensor. For each side of the leaf, the number of stomata in 20 fields of view, each 0.066 mm^2, were counted and averaged for a mean surface value. The microscope was calibrated with a stage micrometer.

The MSU CDC6500 computer was used with the MSU STAT SYSTEM VERSION 4 statistical package to perform the analysis of variance on the conductance and water potential data from this experiment. Two infinitely large conductance values, resulting from a negative or zero resistance measurements were omitted from the analysis as well as two other measurements which were determined to be outliers by the Moshman-Atta range test for outliers (1952) at the 1% level of probability.

The data for those transplants which died during the experiment were substituted with values derived from averaging the values of other individuals of the same species, from the same level, on a given date. Adjustments were made in the appropriate degrees of freedom.

In the greenhouse, diel measurements of stomatal conductances and leaf water potentials were made on August 2-3, 1979, consecutively, on one transplant of S. canadensis, one transplant of S. juncea which was flowering, and two transplants of S. juncea rosettes on August 2-3, 1979. (Due to the destructive nature of the sampling, two rosettes were sampled from alternately during the day.) The four transplants were growing on soil moisture levels 5 or 6. Measurements started in the late evening and progressed into the next day. After sunrise, it became partly cloudy and then rained at 11:00 a.m. It was mostly sunny again by 3:00 p.m.

Seedling measurements of stomatal conductances and leaf water potentials were taken from a leaf of one plant per species, from each of the ten levels where the seedlings had germinated, on the morning of August 24, 1979, a mostly sunny day. The sampling sequence of levels was randomized to minimize the differences between diurnal fluctuations and differential responses to the gradient. In the afternoon, the levels were rerandomized and the experiment was repeated using leaves from different seedlings than those sampled in the morning.

On September 18, 1979, a mostly sunny day, seedling measurements of conductances and water potentials were made on one leaf per species on levels 4, 8, and 12, consecutively, 8 times during the day.

A one way analysis of variance and a two tailed nonparametric Sign Test were used to analyze the data from the diel and the seedling experiments.

RESULTS

Growth rates of S. canadensis transplants were greater than those of S. juncea. Most of the transplant measurements on S. juncea were

made on the rosette stage because after transplanting both species into the gradient boxes, all S. canadensis transplants bolted and only a few of the S. juncea transplants bolted.

For the transplants, values for stomatal conductances and leaf water potential were averaged over two hour time intervals and are presented in Figures 6 and 7 for the four sampling dates (cf. Appendices G, H, I and J). Figure 8 illustrates the mean stomatal conductances and leaf water potentials for all four sampling dates (cf. Appendix K).

Table 2 shows the results of the analysis of variance for the stomatal conductance data for each of the four sampling dates. Table 3 shows the results of the analysis of variance for the leaf water potential data for all four sampling dates. The results for the stomatal conductance and leaf water potential data combined over the four sampling dates are contained in Table 4.

The variables which were included in the analyses were: two species (S. juncea and S. canadensis), two fieldsites ("dry" and "wet"), and four levels (greenhouse soil moisture box levels 3, 6, 9, and 11).

There were significant species differences in leaf water potentials on June 16 and Septemeber 14. Figure 8 illustrates that on June 16, S. juncea reached significantly lower water potentials than S. canadensis (ANOVA, $P<.002$, Table 3) and by the end of the summer S. juncea reached significantly higher water potentials than S. canadensis (ANOVA, $P<.002$, Table 3). Figure 8 also illustrates the significant species x date interaction for leaf water potentials. Figures 6 and 7 show the time course of these species differences in water potentials for June 16 and September 14, respectively.

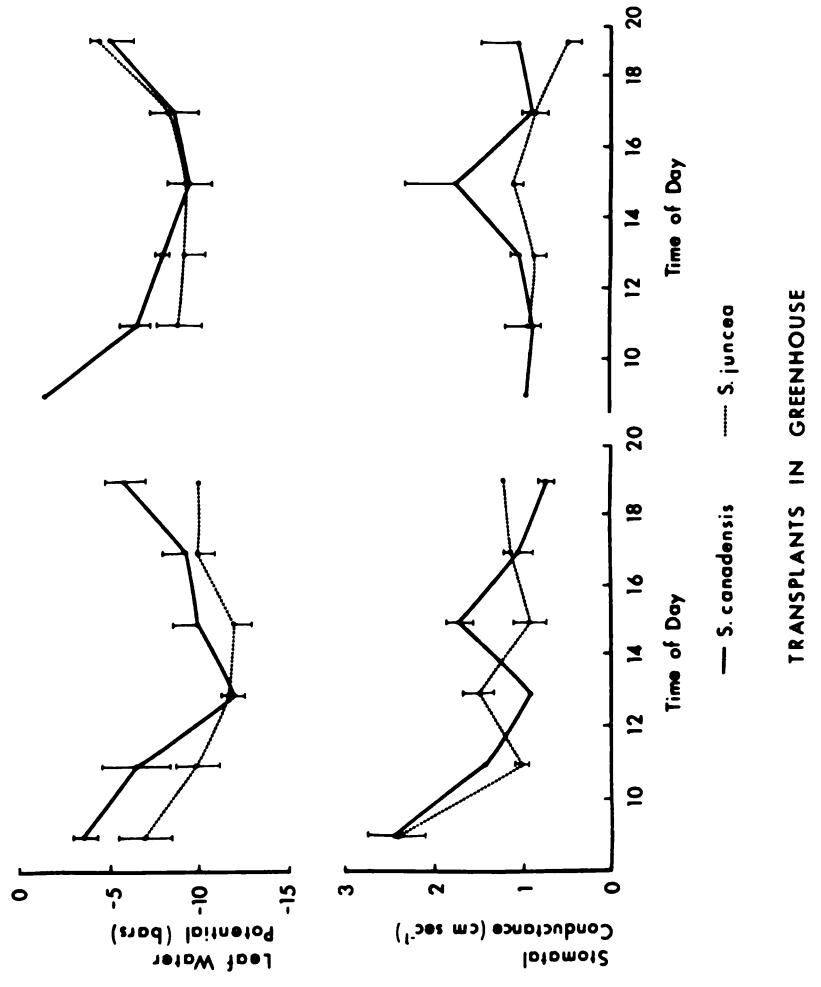

Figure 6. Conductance and Water Potential Measurements: Transplants, June 16, 1979 and June 28, 1979. Data represent means from two hour intervals, vertical bars represent ± 1 S.E.

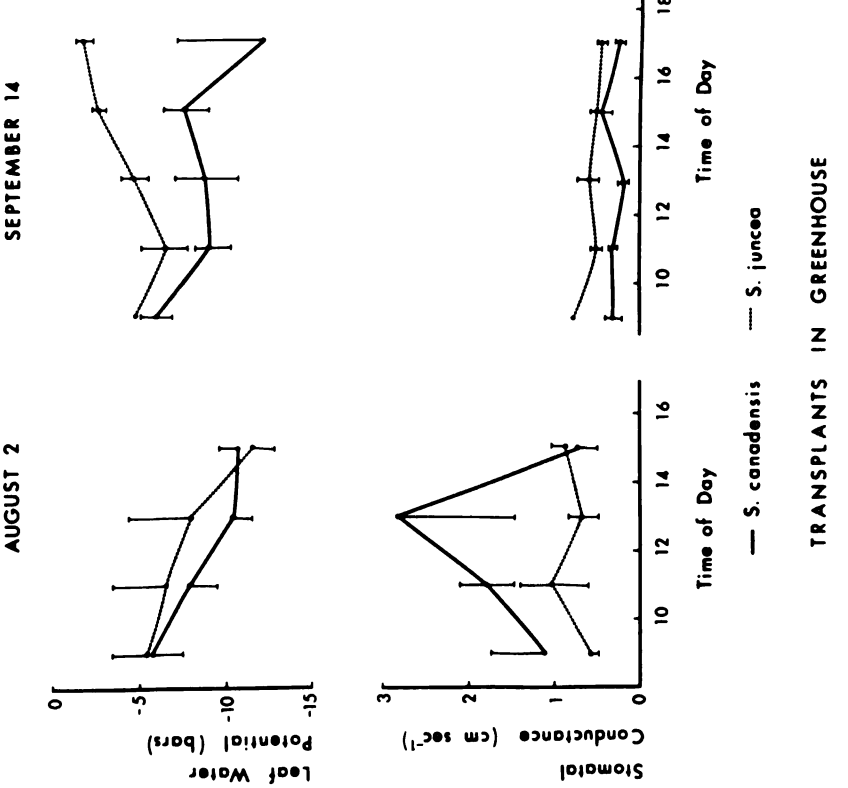

Figure 7. Conductance and Water Potential Measurements: Transplants, August 2, 1979 and September 14, 1979. Data represent means from two hour time intervals, vertical bars represent ± 1 S.E.

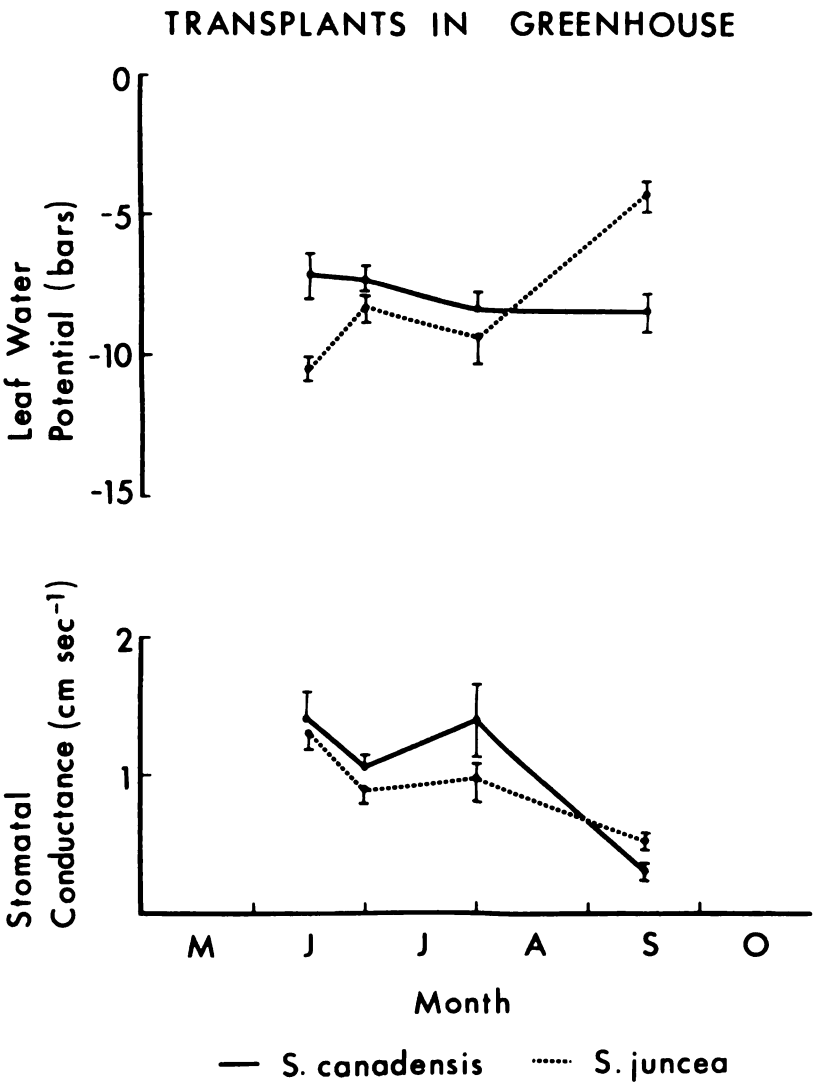

Figure 8. Conductance and Water Potential Measurements: Transplants. Data represent means ± 1 S.E. for all 4 sampling dates.

Table 2. Analysis of Variance: Stomatal Conductance, Transplant Experiments

Sampling date 1, June 16, 1979

source of variation	MS	F	df	P	adjusted for missing values: df	P
species	.190	.336	1	.566	1	p>.5
fieldsite	.008	.014	1	.906	1	p>.5
species x fielsite	.195	.345	1	.561	1	p>.5
level	.366	.648	3	.590	3	p>.5
species x level	.454	.805	3	.500	3	p>.5
fieldsite x level	.862	1.527	3	.226	3	.2<p<.5
species x fieldsite x level	.397	.705	3	.556	3	p>.5
error	.564		32		28	

Sampling date 2, June 28, 1979

source of variation	MS	F	df	P	df	P
species	.392	2.011	1	.166	1	.2<p<.5
fieldsite	.122	.625	1	.435	1	p>.5
species x fielsite	.304	1.558	1	.221	1	.2<p<.5
level	.197	1.013	3	.399	3	.2<p<.5
species x level	.080	.414	3	.744	3	p>.5
fieldsite x level	.014	.075	3	.973	3	p>.5
species x fieldsite x level	.125	.645	3	.592	3	p>.5
error	.195		32		28	

Sampling date 3, August 2, 1979

source of variation	MS	F	df	P	df	P
species	2.227	2.089	1	.158	1	.2<p<.5
fieldsite	.004	.004	1	.949	1	p>.5
species x fieldsite	1.062	.996	1	.326	1	p>.5
level	.341	.319	3	.811	3	p>.5
species x level	1.933	1.813	3	.164	3	.2<p<.5
fieldsite x level	7.47	.700	3	.558	3	p>5
species x fieldsite x level	1.567	1.066	3	.241	3	p>5
error	1.066		32		28	

Sampling date 4, September 14, 1979

source of variation	MS	F	df	P	df	P
species	.537	18.836	1	.0005**	1	p<.002**
fieldsite	.012	.421	1	.521	1	p>.5
species x fielsite	.124	4.345	1	.045	1	.05<p<.1
level	.086	3.022	3	.044	3	.05<p<.1
species x level	.035	1.237	3	.312	3	p>.5
fieldsite x level	.009	.331	3	.803	3	p>.5
species x fieldsite x level	.008	.312	3	.816	3	p>.5
error	.028		32		27	

* = significant below the 0.05 level of probability.
** = significant below the 0.01 level of probability.

Table 3. Analysis of Variance: Leaf Water Potential, Transplant Experiments

Sampling date 1, June 16, 1979

source of variation	MS	F	df	P	adjusted for missing values df	P
species	127.726	13.612	1	.001**	1	p<.002**
fieldsite	14.630	1.559	1	.221	1	.2<p<.5
species x fieldsite	2.755	0.293	1	.592	1	p>.5
level	5.189	0.553	3	.650	3	p>.5
species x level	16.672	1.776	3	.171	3	.2<p<.5
fieldsite x level	6.061	0.645	3	.591	3	p>.5
species x fieldsite x level	5.875	0.626	3	.603	3	p>.5
error	9.383		32		28	

Sampling date 2, June 28, 1979

source of variation	MS	F	df	P	df	P
species	10.640	1,451	1	.237	1	.2<p<.5
fieldsite	4.440	0.605	1	.442	1	p>.5
species x fieldsite	13.440	1.833	1	.185	1	.2<p<.5
level	5.715	0.779	3	.514	3	p>.5
species x level	10.704	1.460	3	.244	3	.2<p<.5
fieldsite x level	3.343	0.456	3	.715	3	p>.5
species x fieldsite x level	10.532	1.436	3	.250	3	p>.5
error	7.331		32		28	

Sampling date 3, August 2, 1980

source of variation	MS	F	d	P	df	P
species	11.701	0.991	1	.327	1	p>.5
fieldsite	11.900	1.007	1	.323	1	p>.5
species x fieldsite	104.725	8.870	1	.005**	1	.01<p<.02**
level	19.896	1.685	3	.190	3	.2<p<.5
species x level	3.401	0.288	3	.834	3	p>.5
fieldsite x level	27.307	2.313	3	.095	3	.1<p<.2
species x fieldsite x level	11.355	0.961	3	.432	3	p>5
error	11.806		32		28	

Sampling date 4, September 14, 1979

source of variation	MS	F	d	P	df	P
species	210.840	23.533	1	.0005**	1	p<.002**
fieldsite	5.333	0.595	1	.447	1	p>.5
species x fieldsite	25.230	2.816	1	.103	1	.2<p<.5
level	7.694	0.858	3	.472	3	p>.5
species x level	3.218	0.359	3	.783	3	p>.5
fieldsite x level	13.948	1.556	3	.219	3	.2<p<.5
species x fieldsite x level	10.379	1.158	3	.341	3	p>.5
error	8,959		32		27	

* = significant below the 0.05 level of probability.
** = significant below the 0.01 level of probability.

Table 4. Combined Analysis of Variance: Stomatal Conductance and Leaf Water Potential Values for All Dates Combined, Transplant Experiments.

source of variation	MS	F	df	P	adjusted for missing values df	P
date	7.857	16.951	3	.0005**	3	p<.002**
species	.829	1.789	1	.183	1	.2<p<.5
date x species	.839	1.810	3	.148	3	.2<p<.5
fieldsite	.094	.203	1	.652	1	p>.5
date x fieldsite	.017	.037	3	.990	3	p>.5
species x fieldsite	.556	1.201	1	.275	1	p>.5
date x species x fieldsite	.376	.811	3	.490	3	p>.5
level	.579	1.249	3	.295	3	p>.5
date x level	.137	.296	9	.975	9	p>.5
species x level	.902	1.947	3	.125	3	.2<p<.5
fieldsite x level	.204	.440	3	.725	3	p>.5
date x species x level	.533	1.151	9	.332	9	p>.5
date x fieldsite x level	.476	1.027	9	.421	9	p>.5
species x fieldsite x level	.349	.752	3	.523	3	p>.5
date x species x fieldsite x level	.583	1.259	9	.265	9	p>.5
error	.463		128		111	

Leaf Water Potentials for Combined Dates

source of variation	MS	F	df	P	df	P
date	64.098	6.840	3	.0005**	3	p<.002**
species	3.000	.320	1	.572	1	p>.5
date x species	119.303	12.732	3	.0005**	3	p<.002**
fieldsite	13.975	1.491	1	.224	1	.2<p<.5
date x fieldsite	7.443	.794	3	.499	3	p>.5
species x fieldsite	74.500	7.950	1	.006	1	.01<p<.02**
date x species x fieldsite	23.883	2.548	3	.059	3	.2<p<.5
level	12.860	1.372	3	.254	3	p>.5
date x level	8.545	.911	9	.517	9	p>.5
species x level	9.650	1.029	3	.382	3	p>.5
fieldsite x level	21.542	2.299	3	.081	3	.1<p<.2
date x species x level	8.115	.866	9	.557	9	p>.5
date x fieldsite x level	9.706	1.035	9	.415	9	p>.5
species x fieldsite x level	12.178	1.299	3	.277	3	p>.5
date x species x fieldsite x level	8.654	.923	9	.507	9	p>.5
error	9.370		128		111	

* = significant below the 0.05 level of probability.
** = significant below the 0.01 level of probability.

On August 2, there was a significant species x fieldsite interaction (Table 3). Solidago canadensis transplants from moist site clones reached higher water potentials than those from drier sites while the transplants of S. juncea from wet site clones reached lower water potentials than those from the dry sites. The species x fieldsite interaction for the combined dates was also significant for water potential values (Table 4).

Stomatal conductance values differed significantly between species on September 14 (see Figures 7 and 8, and Table 2).

Figures 6 and 7 also show the diurnal trends of water potentials with minima occurring in the early afternoon. In these two species, conductances and water potentials seem to be negatively correlated, but there does not seem to be evidence for stomatal closure even when water potentials approach -15 bars.

Stomatal conductance should be a function of the number of stomata on the leaf surface. The mean number of stomata from the leaves in the transplant experiment for the first sampling date (June 16) and the corresponding mean conductances are presented in Table 5 (cf. Appendix L).

These data suggest that although the distribution of stomata on the two leaf surfaces are different for the two species, total numbers of stomata per area are similar on the regions of the leaves used in these experiments and that similar conductances may be associated with this. Solidago canadensis has 95.8% of its stomata on the abaxial surface and S. juncea has 66.0% of its stomata on the abaxial surface.

A regression of mean stomatal number and mean stomatal conductances yields a correlation coefficient of .99 indicating that conductance is

Table 5. Mean Stomatal Numbers and Mean Stomatal Conductances (± 1 S.E.), Transplants, June 16, 1979.

S. canadensis	Stomata / mm^2	Conductance (cm/sec)
adaxial	7.9 ± 2.1	0.08 ± 0.014
abaxial	186.6 ± 11.0	1.42 ± 0.167
S. canadensis	Stomata / $2mm^2$	Conductance (cm/sec)
adax. + abax.	194.6 ± 11.9	1.50 ± 0.17

S. juncea	Stomata / mm^2	Conductance (cm/sec)
adaxial	60.9 ± 7.6	0.41 ± 0.04
abaxial	118.9 ± 12.5	0.87 ± 0.10
S. juncea	Stomata / $2mm^2$	Conductance (cm/sec)
adax. + abax.	179.9 ± 18.7	1.29 ± 0.13

indeed a function of stomatal number for these two species under the conditions in the greenhouse on this sampling date.

The time course of stomatal conductance and leaf water potential values from the greenhouse diel experiment are presented in Figure 9 (cf. Appendix M). The analysis of variance indicated that there were significant differences among species and growth stages in the water potential values, but not in conductances (see Table 6, cf. Appendix N). The Sign Test showed that the S. juncea flowering adult had significantly lower water potentials that S. juncea rosettes (P=.02) and S. canadensis (P=.02). Again, there were no significant differences in conductances.

For each species, seedling establishment did not occur on the two driest resource levels. Solidago juncea germinated before S. canadensis and had more individuals which colonized the drier levels than S. canadensis. Within two weeks though, S. canadensis was taller and appeared more vigorous than S. juncea. Werner (unpublished data) has observed a similar pattern in the same soil moisture boxes. Seedlings of S. canadensis bolted and flowered in the greenhouse while seedlings of S. juncea stayed as rosettes; also, the above ground growth rates of S. canadensis were greater than for S. juncea.

Graphs of stomatal conductances and leaf water potentials, averaged over two hour time intervals, are presented in Figure 10 for the seedling experiments conducted on August 24 and September 18 (cf. Appendices O and Q). On both days, leaves of S. juncea reached lower water potentials than S. canadensis, although these differences are not significant at the .05 level of probability when tested with a one way analysis of variance (Table 7, cf. Appendices P and R). An analysis of

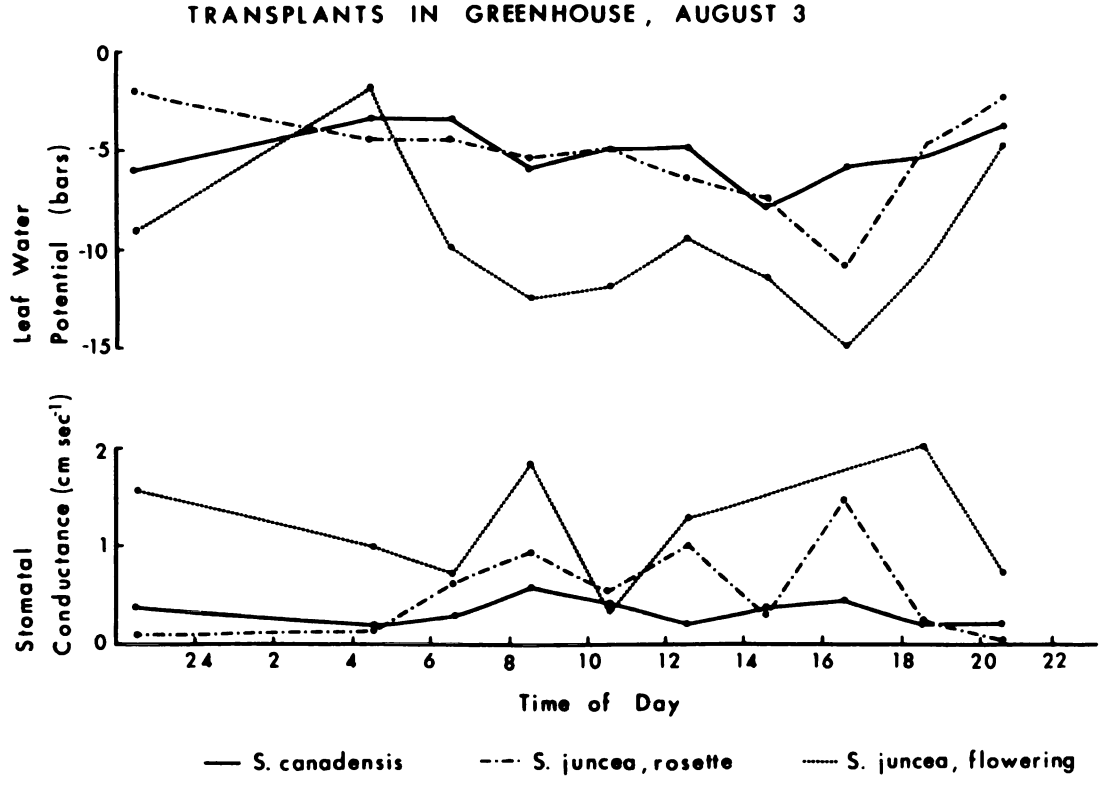

Figure 9. Conductance and Water Potential Measurements: Transplants, Diel, August 2, 1979. Stomatal conductance values for the S. juncea flowering adult at 3:30 and 5:30 p.m. were omitted due to negative resistance measurements.

Table 6. Analysis of Variance, Stomatal Conductance and Leaf Water Potential: Greenhouse Diel, August 2-3, 1979.

Conductance

source of variance	df	MS	F
treatment	2	1.02	3.96
error	27	.25	
total	29		

Water Potential

source of variance	df	MS	F
treatment	2	69.00	8.89**
error	27	7.76	
total	29		

** = significant below the 0.01 level of probability.

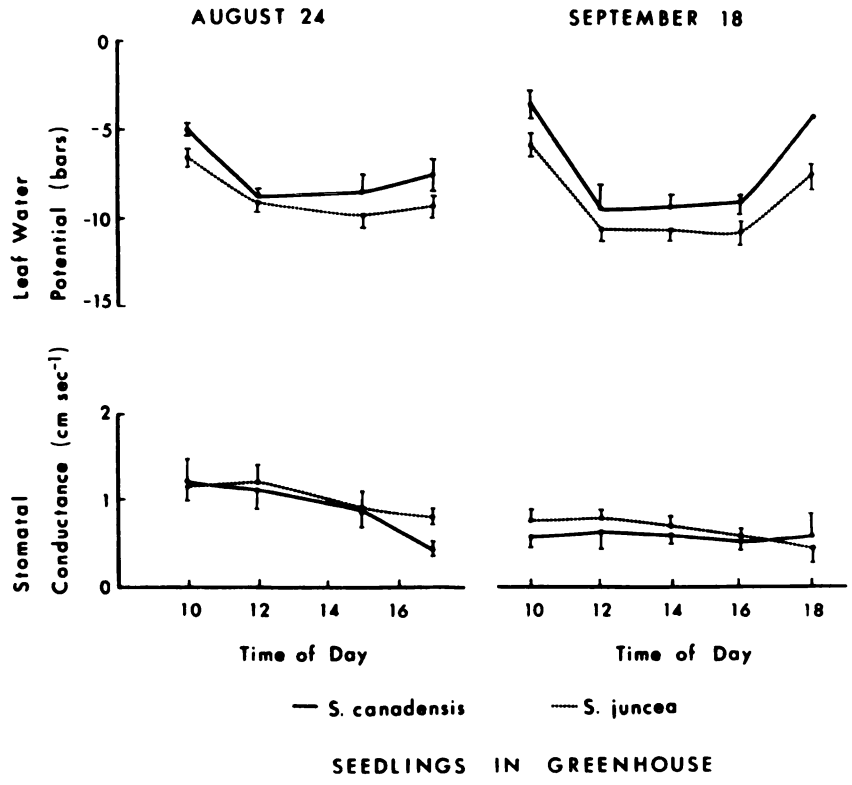

Figure 10. Conductance and Water Potential Measurements: Seedlings, August 24, 1979 and September 18, 1979. Data represent means of two hour time intervals, vertical bars represent $\pm$ 1 S.E.

Table 7. Analysis of Variance, Stomatal Conductance and Leaf Water Potential of Seedlings August 24, 1979 and September 18, 1979.

Conductance 8/24/79

source of variance	df	MS	F
species	1	0.14	.72
error	38	0.19	
total	39		

Water Potential 8/24/79

source of variance	df	MS	F
species	1	12.10	2.98
error	38	4.05	
total	39		

Conductance 9/18/79

source of variance	df	MS	F
species	1	0.09	1.61
error	46	0.59	
total	47		

Water Potential 9/18/79

source of variance	df	MS	F
species	1	34.85	4.10
error	46	8.47	
total	47		

the data with the Sign Test shows that the water potential measurements of S. juncea are significantly lower than those of S. canadensis (P=.002) for both sampling dates. Neither the analysis of variance nor the Sign Test show significant differences in conductances for either sampling date. There were no significant differences in stomatal conductance or leaf water potential responses to the various soil moisture levels in either species.

DISCUSSION

From the soil moisture characteristic curves for the soil moisture gradient (Fig. 5) it can be seen that as the proportion of sand is decreased, similar soil water potentials occur at higher soil moisture contents. The gradient may not be one of drought stress (available water for growth) as much as one of soil moisture content. Determining gravimetric soil moisture content during drying cycles of this gradient, and during experiments, would help to characterize the actual degree of soil moisture stress on this complex gradient.

The lack of significant differences in the stomatal conductances and leaf water potentials of either species in response to the different soil moisture levels in transplant and seedling experiments may be a species' response (i.e. acclimation) or due to the possibility that the actual levels of stress may have been similar for the levels of the gradient from which they were sampled. It is also possible that the plants growing in the greenhouse soil moisture boxes were rarely exposed to differences in soil moisture availability large enough to affect their water use patterns. Values of leaf water potentials from the greenhouse never got as low as those encountered in the field.

With aging, stomata become less responsive and midday stomatal

conductances often decrease because stomata do not open fully (Slatyer and Bierhuizen 1964). Leaf aging could be the cause for the lower conductances of both S. canadensis and S. juncea later in the summer. Since the bolting individuals of both species have determinate growth, no new leaves are produced after flower buds appear and, after a short while, even the most recently produced leaves begin to senesce. On the other hand, rosettes of S. juncea can produce new leaves throughout the summer, but even so, all rosette leaves become brittle at the end of the summer, in the greenhouse, and in the field.

The size, spacing, and number of stomata, even though occupying less than 1% of the leaf surface, allow such efficient gas exchange that diffusion of water vapor through them may approach 50% of the evaporation from a free water surface (van den Honert 1948, Kramer and Kozlowski 1979). Plants which occur in dry areas usually have smaller stomata, more stomata, and have higher densities of them on their adaxial surfaces than mesic plants (Clay and Quinn 1978, Carpenter and Smith 1975, and Tobiesson and Kana 1974). These dry area plants usually have lower conductances, lower transpiration rates, and can maintain net photosynthesis at lower water potentials than more mesic species (Bunce et. al. 1977, Johnson and Caldwell 1976, Bunce 1975, Ehleringer and Miller 1975, Dina and Klikoff 1973, Sanchez-Diaz and Kramer 1971, Anderson 1971, Klickoff 1975, and Bannister 1964). Solidago juncea certainly does have more adaxial stomata than S. canadensis. Their conductances seem to be similar, though, and their photosynthetic response to low water potentials is yet unknown.

Mantuani (1970) in a study of the ecophysiology of goldenrods found that S. californica (a dry site species) had stomata equally

distributed on upper and lower leaf surfaces, while leaves of S. elongata (S. canadensis var. salebrosa, a moist site species) had higher concentrations of stomata on its lower surface. Interestingly, there were no significant differences in the total number of stomata per leaf. S. californica had smaller leaves so the densities per unit area were greater in S. californica.

In this study, S. canadensis had most (96%) of its stomata on the undersurfaces of the leaves. It would be interesting to see if stomatal size and number vary continuously in a genotype of each species grown across the soil moisture gradient and during the season.

In the greenhouse diel experiment, all four transplants showed stomatal opening when conditions became most favorable for photosynthesis (i.e. in the afternoon when the sun reappeared after a shower). This time also corresponds to the time of minimum leaf water potential readings.

The S. juncea flowering adult reached lower leaf water potentials than the S. juncea rosettes or the S. canadensis individual. Again, as in the field diel study (Chapter 1), this could be due to a change in the morphology or physiology of the plant during flowering. In the greenhouse study, though, the lower water potentials of the S. juncea flowering individual were accompanied by high stomatal conductances. This also suggests that assimilation rates may have been higher in this particular plant.

The sample size was small in this experiment, and the differences in leaf water potentials and stomatal conductances may reflect individual plant differences rather than species' differences. Still, the diel patterns of leaf water potentials were evident with afternoon

minima which coincided with peak evaporative demand.

The physiological measurements indicate that leaves of S. juncea seedlings reach lower leaf water potentials during the day than those of S. canadensis. Since stomatal conductances per unit leaf area are similar, the larger leaf size of the S. juncea rosette may be a morphological basis for these higher levels of stress. A larger leaf presents more surface area for transpiration and, given similar stomatal conductances, a larger leaf may lose more water than a small leaf. This would result in lower leaf water potentials even if conductances were similar per unit leaf area.

The seedlings of both species were growing close enough to their conspecifics (1.5 seedlings dm^{-2}) for intraspecific competition for soil moisture to occur. Lowered leaf water potentials would result if the roots could not supply water to the above ground parts at a sufficient rate. If soil water depletion occurred at a faster rate on the side of the gradient where S. juncea was growing, then lower leaf water potentials would be expected. This condition of lower leaf water potentials in S. juncea seedlings would also occur if S. juncea had higher root resistances than S. canadensis.

Small increases in stomatal conductances may cause large changes in leaf water status. Although not significantly different, the mean conductance for S. juncea was higher than that for S. canadensis on both seedling sampling dates. Since the exact relationship between conductance and the development of water stress in these plants is unknown, this "slightly" higher conductance may be very important to the water balance of the plant and could cause significantly lower leaf water potentials.

CHAPTER III. LABORATORY STUDIES

METHODS

In October 1979, plants of S.juncea and S. canadensis which had been growing on the soil moisture gradient in the KBS greenhouse were potted, using the soil that they had been growing in, and transferred to a growth chamber in the MSU-DOE Plant Research Laboratories.

In the growth chamber, the daylength was 20 hrs and the highest of three light intensities was 230 w m^{-2} between 400-700 nm. The day temperature was 24 C; the night temperature was 20 C and the relative humidity was 75%. In early Feb., 1980, the growth chamber conditions were altered to a 27/20 C day/night temperature.

An infra red gas analysis system designed by K. Raschke (DOE Laboratory, MSU, see Farquhar and Raschke 1978, for a more detailed description of the apparatus) was used to measure assimilation rates, evaporation rates, and stomatal conductances on leaves of S. juncea and S. canadensis.

Freshly detatched leaves were mounted in aluminum leaf chambers through which water of 25 C was pumped to control the air temperature. Air of known water vapor content (dew point = 18.5 C) and CO_2 content (300 $\pm$ 8 microliters $liter^{-1}$) was passed over each leaf surface at 50 liters hr^{-1} and then sent through IR gas analyzers. The chambers allowed 2.44 cm^2 of leaf area to be exposed to the air stream.

Molar fluxes of CO_2 and H_2O for the upper and lower leaf surfaces

were measured using four differential gas analyzers (Uras; Hartmann und Braan, Frankfurt, a.M., Germany). The absolute CO_2 content of the air was monitored with an additional Uras. Thermocouples were used to measure leaf temperature and the temperature of the condensor setting the dew point of the air supplied to the chambers.

Voltages from the thermocouples and the gas analyzers were fed into a minicomputer which calculated assimilation rates, evaporation rates, and conductances (stomatal and boundary layer together).

The light source was a water cooled xenon arc lamp (Osram XBF 6000 w) behind IR absorbing glass filters (Corning 4600). Neutral density filters (Plexiglass No. 800 and 838 Rohm und Haas, Darmstadt, Germany) were used to vary the light intensity. The irradiance was monitored with a silicon cell in the same plane as the leaf chambers.

Leaves used in this experiment were cut and recut underwater and the petioles of the leaves were kept in a beaker containing distilled water throughout the experiment. Measurements on the leaves were completed within 3½ hrs after the leaves were cut. The leaves used were the 6th or 7th from the apex of S. canadensis and the 4th or 5th from the apex of rosettes of S. juncea. Values of assimilation, evaporation and stomatal conductances are combined values from the upper and lower epidermis and are expressed per unit leaf area.

Experiments where the light intensity was varied from 0-800 w m^{-2} were conducted in December, 1979, and March, 1980, on a total of 9-10 leaves of each species. Readings on each leaf were taken every 5 min. Values of assimilation rates, evaporation rates, and stomatal conductances are averages from 15 min time spans after the leaves reached a steady state, i.e. stabilized stomatal conductances.

Because the gas analyzers were recalibrated during the experiment, average percent of maximum values are reported in this study in addition to absolute values. The maximum value of assimilation for each leaf was used to calculate the percent of maximum assimilation for that leaf at each light intensity. Then for all leaves of each species an average of these values was calculated for each light level. This same procedure was used to calculate the average percent of maximum stomatal conductance and the average percent of maximum water use efficiency (WUE).

RESULTS

The average maximum assimilation rates and associated standard errors were 13.25 $\pm$ 1.06 micromoles CO_2 m^{-2} sec^{-1} for S. juncea and S. canadensis respectively. These assimilation rates correspond to 20.98 mg dm^{-2} hr^{-1} for S. juncea and 20.78 mg dm^{-2} hr^{-1} for S. canadensis. These values were calculated for 9-10 leaves of each species. Figure 11 illustrates the typical light saturation curves for the absolute assimilation rates of two leaves of each species at the various light intensities (cf. Appendix S). Figure 12 illustrates the average percent of maximum assimilation rates for both species at the different light intensities (cf. Appendix 2).

The average maximum stomatal conductances ($\pm$ 1 standard error) for S. juncea and S. canadensis were 38.44 $\pm$ 3.30 centimoles H_2O m^{-2} sec^{-1} and 31.53 $\pm$ 2.59 centimoles H_2O m^{-2} sec^{-1} (.96 cm sec^{-1} and .78 cm sec^{-1}) respectively. The average percent of maximum stomatal conductance at the various light intensities are presented in Figure 13 (cf. Appendix T). The conductance measurements in the laboratory are consistent with the readings made in the greenhouse and in in situ

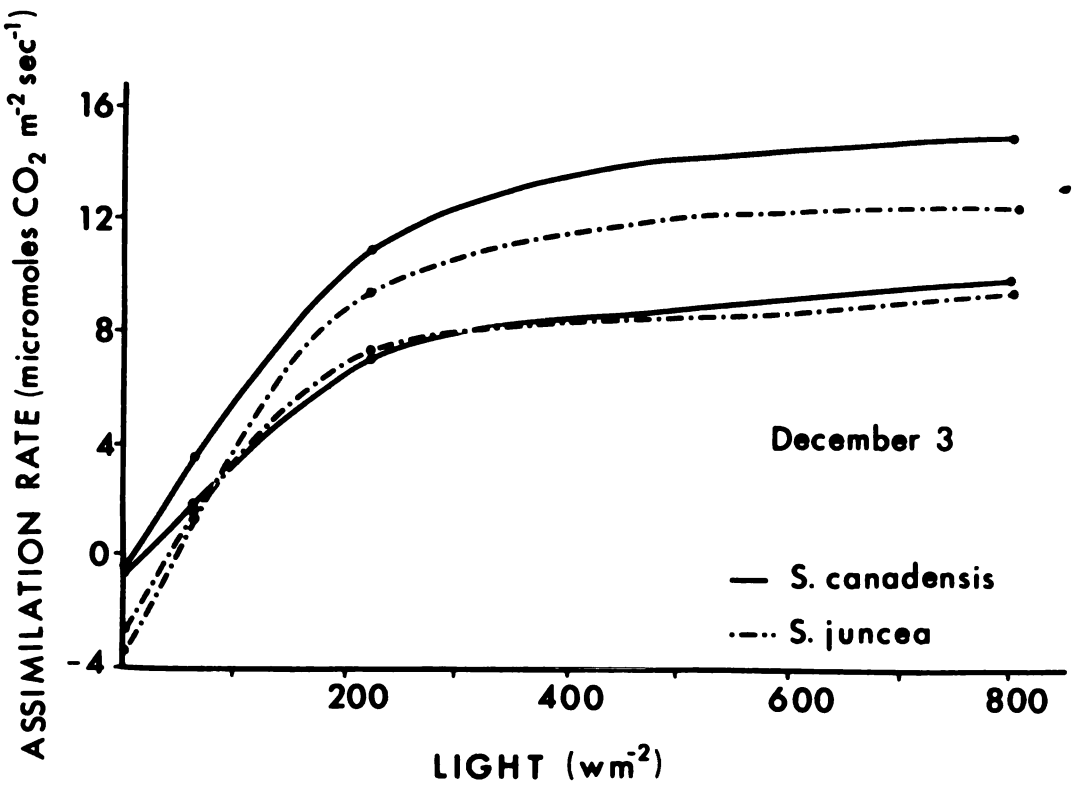

Figure 11. Absolute Assimilation Rates as a Function of Light Intensity for Two Leaves of Solidago canadensis and S. juncea.

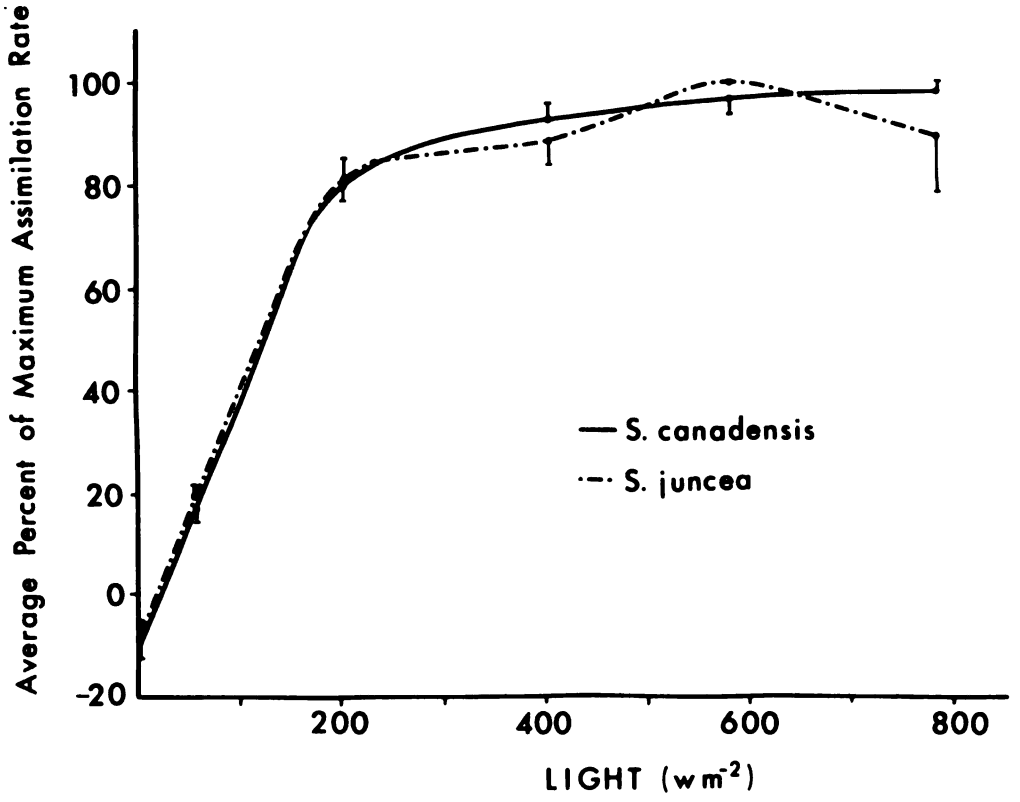

Figure 12. Average Percent of Maximum Assimilation as a Function of Light Intensity for Solidago canadensis and S. juncea. Values are averages ± 1 S.E. for 9-10 leaves of each species.

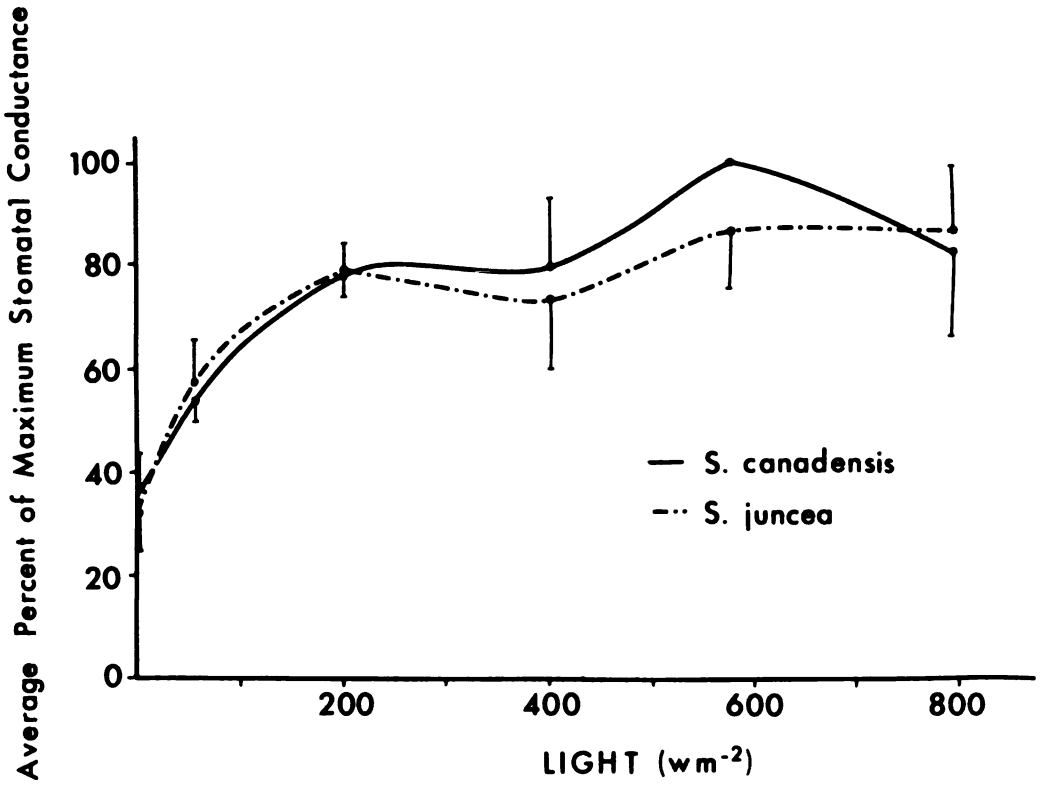

Figure 13. Average Percent of Maximum Stomatal Conductance as a Function of Light Intensity for Solidago canadensis and S. juncea. Values are averages ± 1 S.E. for 9-10 leaves of each species.

experiments (see Chapters I and II).

The average maximum WUE (water use efficiency) and associated standard errors are 3.32 ± .32 micromoles CO_2 millimoles H_2O^{-1} (8.10 mg CO_2 gH_2O^{-1}) for S. juncea and 3.96 ± .24 micromoles CO_2 millimoles H_2O^{-1} (9.66 mg $CO_2 \cdot gH_2O^{-1}$) for S. canadensis. The average percent of maximum WUE at the various light intensities are presented in Figure 14 (cf. Appendix U). These data indicate that at high light levels, S. juncea may photosynthesize at a higher percent of maximum WUE than S. canadensis, even though its average maximum WUE is less than that of S. canadensis.

Analysis of these data with the Sign Test showed no significant differences (at the .05 level of probability) between species in average percent of maximum assimilation, conductance, or WUE across the range of light intensities.

DISCUSSION

The stomata of both S. juncea and S. canadensis show the characteristic photoactive opening response to light. As the stomata open, gas exchange occurs and assimilation rates increase. The stomatal response to light intensity is mainly a result of their sensitivity to the concentration of CO_2 in the air spaces of the leaf (Raschke 1975). With increased illumination, CO_2 uptake increases in proportion to the light intensity at first, and then more slowly to a maximum value. This is characteristic of light saturation curves. In the dark, the relationship is negative because of the net release of CO_2 (more CO_2 is given off by respiration than is fixed by photosynthesis). As light intensity increases, the speed of the light reactions is a function of the light intensity. As light intensity increases further, enzymatic

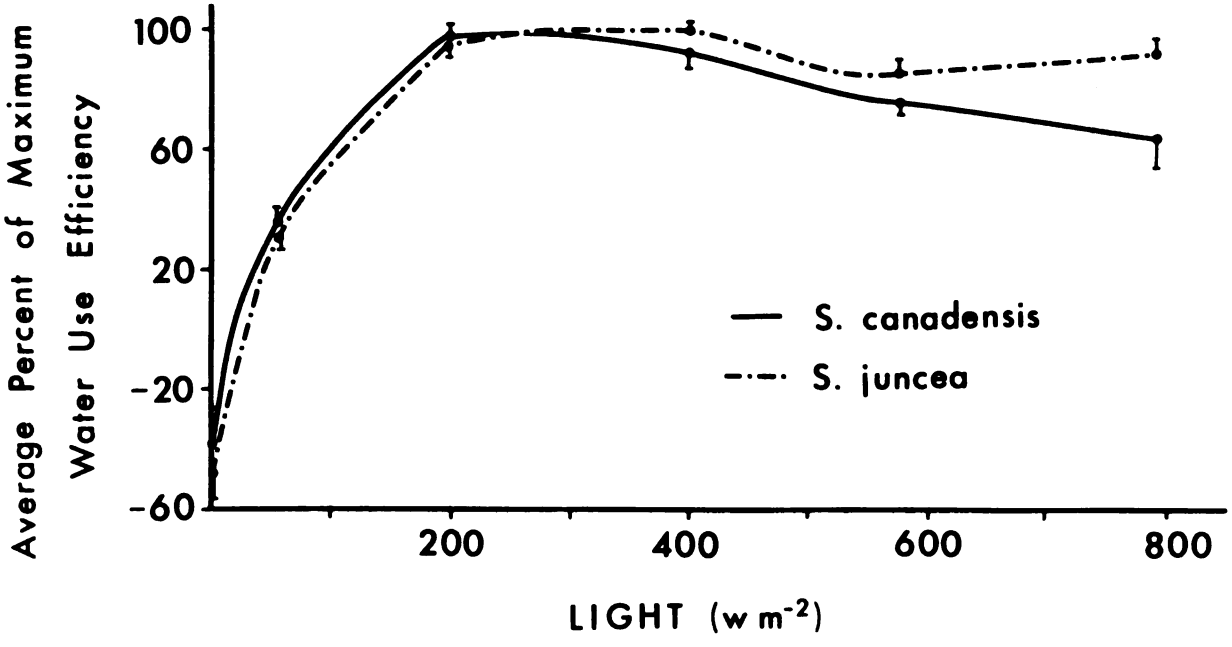

Figure 14. Average Percent of Maximum Water Use Efficiency as a Function of Light Intensity for Solidago canadensis and S. juncea. Values are averages ± 1 S.E. for 9-10 leaves of each species.

limitations are approached and sometimes light reactions may be inhibited by high light intensities.

With increasing light intensities, increased respiration also occurs in C_3 plants. This probably accounts for the peak in WUE which occurs at or about the light intensities used in the growth chambers (230 wm^{-2}, about half the intensity of full sunlight). The highest efficiencies occur at about the maximum light intensities in the growth chambers. Plants from the field which are exposed to full sunlight, about 500 wm^{-2} (Campbell 1977), would probably have their maximum WUE's at higher light intensities because the development of the leaf, including its photosynthetic "machinery" are influenced by ambient light intensities.

It is not necessarily true that high photosynthetic rates will result in the production of more dry matter and more rapid growth rates than plants with a low photosynthetic rate (Carter 1972). Helms (1976) reviewed the difficulties in relating growth rate to photosynthetic rate in trees, and Evans (1975) gives evidence that these difficulties exist in herbaceous plants. Growth (dry matter production) is a function of photosynthetic rate, leaf area, and leaf age, all of which change during the season. Both S. juncea and S. canadensis have similar assimilation rates but the higher stomatal conductances of S. juncea result in a lower WUE.

Compared with many crop species the stomatal responses of single leaves of these goldenrods were very variable (K. Raschke, personal communication). This variability in response is consistent with the large differences in leaf measurements from both the field and greenhouse studies (see Chapters I and II).

The similarity in the assimilation rates of these two species may reflect their close evolutionary and/or successional relationships. Based on their average maximum assimilation rates alone (20.9 and 20.7 mg dm^{-2} h^{-1} for S. juncea and S. canadensis respectively), these two species could be categorized as herbaceous heliophytes (20-50 mg dm^{-2} h^{-1}) or agricultural C_3 plants (20-40 mg $dm^{-2}h^{-1}$) (Larcher 1975). According to a recent review of the physiological ecology of plant succession (Bazzaz 1979) these plants have assimilation rates similar tosuccessional plants which inhabit old-fields, even as high as some summer annuals.

GENERAL DISCUSSION

A. Physiology: Water Use

There are basically two types of mechanisms involving stomatal closure, to control plant water balance. The first is the avoidance of large changes in water content and osmotic potentials during the day by sensitive stomatal control over the rate of water loss. Plants with this mechanism have some means of storing water in various plant parts and are represented by trees, succulents, shade plants, and some grasses. The second is a tolerance mechanism which allows wide fluctuations in osmotic potentials and water content during the day with restricted transpiration through stomatal control only if conditions become excessively dry. Plants with this drought response must have protoplasms which can tolerate these fluctuations in osmotic concentration and in water potential. Many herbs which occur in sunny habitats have this tolerance mechanism. (Some plants completely lack stomatal closure in response to mild water stress, a characteristic which could restrict them to habitats with a constant water supply; such is the case for Populus tremuloides (Tobiesson and Kana 1974)).

A nonstomatal mechanism of controlling the deleterious effects of water stress is through osmoregulation. The data presented in the in situ diel study (Chapter I) indicates that this mechanism may be operating in both species of goldenrods.

Both S. canadensis and S. juncea fit into the drought tolerant

category. Stomatal conductances and leaf water potentials indicate that they lose water during the day without stomatal closure. Levels of plant moisture stress witnessed in the field and in the greenhouse, during the day when the light levels were high, may not have been severe enough to trigger stomatal closure in either of these species. Laboratory experiments indicated an opening response of stomata to light. In the field and in the greenhouse experiments, measurements were never made on the same leaf twice, so definite opening and closing responses of stomata may have been masked by variability due to leaf age, stomatal number or variability in response from one individual to another.

In a study of two species of non-co-occurring goldenrods in California (Mantuani, 1970) the dry site species (S. californica) exhibited drought avoidance behavior by closing its stomata early in the day and at high leaf water content. Stomatal closure occurred in response to minimum leaf water potentials of -15 to -20 bars. When both species were exposed to similar drought conditions in the laboratory, the moist site species (S. canadensis spp. elongata = S. canadensis var. salebrosa; Scoggan 1979) did not close its stomata and, where it was growing in the field, experienced little drought stress during the summer.

This lack of stomatal closure in S. canadensis var. salebrosa is consistent with the results of the present study of S. canadensis var. scabra. Since S. canadensis and S. juncea occur in the same old-field in Michigan, it is expected that they would have more similar physiological mechanisms of coping with environmental fluctuations than the two species (Mantuani 1970) which occur in markedly different

habitats.

Since assimilation rates were measured per unit leaf area under controlled conditions and since leaf size, leaf temperature, leaf age, potential of an individual plant (ramet or genet in the case of cloning perennials) then care must be taken when extrapolating from data gathered from single leaves to the whole plant or to a stand of plants and from greenhouse and growth chamber grown plants to those in the field. Without knowing the total carbon balance of these two species from physiological data one can only speculate on their relative competitive abilities.

High assimilation rates do not necessarily result in high growth rates. The allocation of assimilates to above and below ground structures and vegetative and sexual reproduction differs from species to species. Respiration rates may change at different stages in the life cycle of a species. Flowers and unripe fruit, for example, typically have high respiration rates (Larcher 1975) which would decrease net photosynthesis and possibly growth. Givnish (1979) recently warned that selection probably does not maximize photosynthetic rates in plants, as assumption which is present in many current models which attempt to predict results of competitive interactions and/or species' distributions.

The slight differences in the patterns of water use and assimilation rates of these two species may be of minor importance to the total carbon balance and competitive ability of these two species when compared to differences in morphological, phenological and life history characteristics, and the plasticity of the responses associated with them.

B. Morphology: Relationship to Water Use

The maintenance of the rosette form may allow survival of S. juncea on drier sites but this may also result in its lower competitive ability. This competitive disadvantage becomes apparent when this species is placed or germinates on moister sites with competitors. A comparison of the rosette and the flowering adult habit suggests that there are costs as well as benefits associated with each habit which could affect competitive ability.

Since the rosette habit limits the height that an individual ramet can attain, rosettes of S. juncea often become overtopped and shaded by neighboring plants when they occur on moister sites (Werner, unpublished data). They rarely become shaded on drier sites where there is less competition for light. The rosette habit requires less biomass to produce than a tall, leafy individual.

The short rosettes influence and are influenced by the climate near the ground more than taller plants. The increase in humidity and the decrease in wind speed near the ground surface tends to decrease transpirational water loss. The spacing and leaf arrangement of the rosettes influences the evaporative water loss from the soil.

Leaf size and arrangement are important factors in plant water balance. The rosette leaves of S. juncea are fewer and larger than the leaves of the flowering stems and those of S. canadensis. With similar stomatal conductances per unit area the larger surface area of a single large leaf would cause it to lose more water and would result in higher levels of water stress than a smaller leaf. There seems to be evidence for this from greenhouse seedling experiments (Chapter II). Both species had similar stomatal conductances per unit leaf area, but S.

juncea had lower leaf water potentials than S. canadensis.

A rosette of leaves may lose less water via transpiration than a bolting upright form, giving it an advantage on drier sites. With a smaller total leaf area, though, the net photosynthesis for a rosette might be lower than for a bolting individual.

Associated with larger leaves are thicker boundary layers. As boundary layer thickness increases, the resistance to gaseous diffusion increases which results in a simultaneous reduction in the transpiration rate and an increase in leaf temperature. Rosette leaves of S. juncea are protected from leaf overheating by the lack of stomatal closure at high leaf water potentials. The distribution of stomata on both sides of the leaf also allows for more efficient gas diffusion and heat transfer in the leaf.

Since respiration rates increase with increasing light intensities, maximum WUE (water use efficiency) is usually reached at some intermediate light level. The erect arrangement of the leaves in a rosette would decrease the effective light intensity that reaches the leaf surface allowing a higher WUE than horizontal leaves, at high light intensities.

The bolting ramets of S. juncea face little competition for light because they arise from among the short rosettes. As the summer progresses and the soil becomes progressively drier, the flowering stems produce smaller leaves which have smaller boundary layers and more efficient heat and gas exchange.

The root systems of the S. juncea and S. canadensis source clones used in the diel study (Chapter I) were partially excavated at the end of the summer for a comparison of their root morphologies. Both species

had both small fibrous roots in the upper 10 cm of soil and deep, mostly unbranched roots below. At the edges of the clones the fibrous roots were mingled with those of the adjacent vegetation but roots growing as deep as those of the goldenrod's were not evident. The deep root systems and the clonal habit prevent overlap of their root systems with those of neighboring plants. These deep, non-overlapping root systems allow these two species to tap otherwise untouched water resources.

In general, if a plant has a high WUE and a shallow root system and grows among less water use efficient plants, then the soil water conserved by its efficient water use will be spent by the adjacent plants whose roots tap the same resources. Unless this high WUE strategy were associated with the ability to extract water at low soil water potentials, there would be no selective pressure to maintain efficient water use under these conditions.

C. Phenology

With its earlier flowering time and slower growth rates, S. juncea flowering stems do not get as tall as those of S. canadensis. In a field population of S. juncea, flower buds appeared by July 5 compared to August 30 for S. canadensis. Bud formation for S. juncea occurred before the onset of soil water depletion (see Chapter I). Because of its indeterminate growth pattern, this means that S. juncea was able to complete most of its vegetative growth when soil moisture conditions were favorable for growth. It is possible that the rosette stage is necessary to allow the accumulation and storage of the assimilates needed to allow early flowering in the following year. The maintenance

of a vegetative rosette and an early flowering reproductive stage could be a mechanism to escape drought stress.

In comparison to S. juncea, S. canadensis has a faster above ground growth rate. It has no rosette stage and seems to be efficient in converting available water and nutrients into new photosynthetic structures to further increase its above-ground height and biomass. With its high total surface area and fairly high conductances, it would require large amounts of water for growth. This high water demand may restrict it to moist sites.

During the summer, S. canadensis seems to invest assimilates into above-ground biomass, and height, making it a good competitor for light, and then flowers when allbut a few Asters are finished flowering, and when the seasonal evaporative demand at midday has begun to decrease, day lengths are shorter, light intensities are lower; and temperatures are cooler.

Observations of the germination patterns of these two species on a soil moisture gradient indicate than when conditions are favorable for germination, S. juncea germinates faster and under drier conditions than S. canadensis. As a seedling though, S. juncea, with a slower growth rate, is soon overtopped and shaded if grown with S. canadensis on moist sites (Werner unpublished data). On the other hand S. juncea may persist on the drier sites where S. canadensis is unable to become established.

CONCLUSIONS

Despite small diurnal and seasonal differences, both S. canadensis and S. juncea have relatively similar water use patterns. Both maintain open stomata at leaf water potentials of -20 bars and are characterized as drought tolerant species. Their high assimilation rates, conductances and WUE's are characteristic of early successional species.

Even though they seem suited to grow on similar sites, the potential distribution of S. juncea is greater than its actual distribution indicates. Morphological, phenological and life history differences are likely more important than differences in their water use patterns in causing the observed distributional patterns of S. canadensis and S. juncea.

From this and other studies (Werner unpublished) I would hypothesize that competitive displacement (biotic stress) restricts the occurrence of S. juncea on moister sites with light being the limiting factor and that on the dry sites, S. canadensis is limited by the amount of available water (abiotic stress) for the maintenance of its high growth rates.

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APPENDICES

APPENDIX A

Soil Characteristic Curves: Fieldsites. Values given are percent soil moisture.

	Soil Water Potential					
	15 bars	5 bars	1 bar	.3 bar	.08 bar	.06 bar
Fieldsite 1 (driest)	4.68%	5.61%	8.14%	10.58%	13.31%	14.91%
Fieldsite 2	4.26	5.26	8.05	11.46	14.48	16.09
Fieldsite 3	5.73	6.68	8.81	11.46	14.77	15.38
Fieldsite 4 (wettest)	5.38	6.16	9.40	12.23	14.88	16.12

APPENDIX B

Seasonal Soil Moisture Curves for 1979: Fieldsites. Values given are percent soil moisture.

	Apr.27	June 9	July 5	July 24	Sept.5	Sept.20
Fieldsite 1 (driest)	15.93%	12.52%	12.45%	2.71%	9.43%	4.62%
Fieldsite 2	17.07	13.51	14.36	2.98	11.58	4.38
Fieldsite 3	16.68	12.75	13.11	3.44	9.99	3.57
Fieldsite 4 (wettest)	17.18	14.52	14.85	4.32	12.57	5.40

APPENDIX C

Daily Precipitation During the Summer of 1979.

June	Rain (in.)	July	Rain (in.)
1	trace	1	.30
5	.04	4	1.35
7	.70	14	trace
8	2.33	24	trace
10	1.53	25	.05
18	trace	26	trace
20	1.37	28	.03
21	.02	30	.45
28	.70	31	.10
29	1.36		
30	1.23		

August	Rain (in.)	September	Rain (in.)
1	.18	4	trace
2	.15		
4	.54		
5	.45		
8	.07		
9	.12		
10	.77		
13	.03		
14	.04		
17	.75		
18	.64		
20	.17		
23	.75		
24	.12		
27	trace		
29	.21		

APPENDIX D

Field Diel Measurements of Stomatal Conductances and Leaf Water Potentials at Fieldsite 2 (dry), September 6, 1979. Data represent means for 2 hour intervals ± 1 standard error.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	N	Leaf Water Potential (bars)	N
6-8	*S. canadensis*	1.16 ± .47	3	2.00 ± .28	3
	S. juncea, flowering	.36 ± .04	2	4.50 ± 1.49	2
	S. juncea, rosette	.91 ± .25	2	1.25 ± .24	2
8-10	*S. canadensis*	.74 ± .27	3	8.16 ± 4.05	3
	S. juncea, flowering	.38 ± .03	4	9.75 ± 3.53	4
	S. juncea, rosette	.75 ± .08	3	5.66 ± 2.66	3
10-12	*S. canadensis*	.56 ± .03	7	13.42 ± 1.75	7
	S. juncea, flowering	.56 ± .06	7	15.00 ± .68	7
	S. juncea, rosette	.57 ± .06	8	14.06 ± 1.47	8
12-14	*S. canadensis*	.74 ± .06	3	14.00 ± 1.03	3
	S. juncea, flowering	.62 ± .03	2	15.25 ± 1.24	2
	S. juncea, rosette	.34 ± .09	3	11.50 ± 2.49	2
14-16	*S. canadensis*	.57 ± .18	3	16.83 ± 2.34	3
	S. juncea, flowering	.52 ± .09	3	15.87 ± 2.09	4
	S. juncea, rosette	.43 ± .09	4	17.37 ± .55	4
16-18	*S. canadensis*	.51 ± .06	8	13.68 ± 2.04	8
	S. juncea, flowering	.58 ± .09	7	17.07 ± 1.31	7
	S. juncea, rosette	.41 ± .03	7	16.14 ± .99	7
18-20	*S. canadensis*	.66	1	13.00	1
	S. juncea, flowering	.50 ± .18	2	12.25 ± .74	2
	S. juncea, rosette	.27 ± .01	2	8.00 ± 2.99	2
20-22	*S. canadensis*	.31 ± .07	4	5.25 ± .43	4
	S. juncea, flowering	.50 ± .13	4	6.37 ± 1.97	4
	S. juncea, rosette	.47 ± .08	4	5.62 ± 1.74	4
0-2	*S. canadensis*	1.15 ± .26	4	6.75 ± 1.53	4
	S. juncea, flowering	1.16 ± .36	4	7.12 ± .89	4
	S. juncea, rosette	1.10 ± .31	3	3.33 ± .87	3
2-4	*S. canadensis*	.34	1	3.50	1
	S. juncea, flowering	.75	1	3.00	1
	S. juncea, rosette	.89	1	3.50	1

APPENDIX E

Analysis of Variance: Field Diel Measurements of Stomatal Conductance and Leaf Water Potentials.

Leaf Water Potential (bars)

S. canadensis	*S. juncea*, flowering	*S. juncea*, rosette
$n = 37$	$n = 37$	$n = 36$
$\bar{X} = 10.56$	$\bar{X} = 12.10$	$\bar{X} = 10.81$
S.D. = 5.97	S.D. = 5.57	S.D. = 6.20
$\Sigma X_i^2 = 5419$	$\Sigma X_j^2 = 6545$	$\Sigma X_k^2 = 5559.75$
$\Sigma X_i = 391$	$\Sigma X_j = 448$	$\Sigma X_k = 389.5$

Treatments = 3
Replications = 37

$$\text{Correction term} = \frac{(391 + 448 + 389.5)^2}{(3)(37)} = 13596.5$$

Total SS = 6545 + 5419 + 5559.75 - 13596.5 = 3927.25

$$\text{Treatment SS} = \frac{391^2 + 448^2 + 389}{37} - 13596.6 = 60.1$$

Error SS = 3927.25 - 60.1 = 3867.15

Source of variance	df	MS	F	
treatment	2	30.5	.85	n.s.
error	108	35.80		
total	110			

APPENDIX E (Continued)

Stomatal Conductance (cm sec^{-1})

S. canadensis	*S. juncea*, flowering	*S. juncea*, rosette
$n = 37$	$n = 36$	$n = 36$
$\bar{X} = .67$	$\bar{X} = .60$	$\bar{X} = .55$
S.D. = .40	S.D. = .35	S.D. = .29
$\Sigma X_i^2 = 22.62$	$\Sigma X_j^2 = 17.29$	$\Sigma X_k^2 = 14.21$
$\Sigma X_i = 24.96$	$\Sigma X_j = 1.61$	$\Sigma X_k = 20.08$

Treatments = 3
Replications = 37

$$\text{Correction term} = \frac{(24.96 + 21.61 + 20.08)^2}{(3)(36)} = 41.13$$

Total SS = 22.62 + 17.29 + 14.21 - 41.13 = 12.99

$$\text{Treatment SS} = \frac{24.96^2 + 21.61^2 + 20.08^2}{36} - 41.13 = .34$$

Error SS = 12.99 - .34 = 12.65

Source of variance	df	MS	F	
treatment	2	.17	1.41	n.s.
error	105	.12		
total	107			

APPENDIX F

Soil Characteristic Curves: Experimental Gradient Boxes in the Greenhouse. Values given are percent soil moisture. Data represent means of two replicates.

Soil Water Potential

Soil Moisture Level	15 bars	11 bars	5 bars	1 bar	0.5 bar
1	0.24	0.03	0.02	0.80	0.51
2	1.53	1.18	.89	2.17	2.00
3	3.77	3.37	3.33	5.82	5.23
4	8.11	7.34	6.90	10.29	8.60
5	9.43	8.27	9.59	10.15	10.70
6	10.27	10.48	9.87	11.68	13.09
7	17.50	14.42	17.90	18.87	19.75
8	19.97	18.12	18.54	23.16	22.10
9	21.93	21.82	20.11	26.01	24.19
10	24.10	23.44	22.98	25.81	25.77
11	27.71	29.82	29.41	33.11	33.22

Soil Water Potential

Soil Moisture Level	.3 bar	.2 bar	.1 bar	.05 bar	.02 bar
1	1.07	.87	1.10	1.32	2.94
2	2.24	2.59	2.50	3.09	4.66
3	5.65	6.47	7.28	8.04	10.07
4	9.52	10.35	11.59	10.67	16.39
5	12.05	12.96	14.39	14.76	19.83
6	12.90	12.91	16.92	16.63	21.55
7	19.02	20.99	22.37	24.13	29.84
8	22.93	25.80	25.88	31.32	33.89
9	25.75	27.24	29.24	30.40	35.20
10	27.42	31.99	32.70	34.03	35.63
11	33.45	37.79	37.35	40.20	43.13

APPENDIX G

Greenhouse Stomatal Conductance and Leaf Water Potential Measurements: Transplants, Sampling Date 1, June 16, 1979. Data represent means from two hour intervals ± 1 standard error.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	N	Leaf Water Potential (bars)	N
8-10	S. canadensis	2.45 ± .32	6	3.64 ± .68	7
	S. juncea	2.42 ± .32	3	7.00 ± 1.49	3
10-12	S. canadensis	1.42	1	6.50 ± 1.99	2
	S. juncea	1.01 ± .03	3	9.83 ± 1.47	3
12-14	S. canadensis	.91	1	12.00	1
	S. juncea	1.52 ± .16	4	11.87 ± .65	4
14-16	S. canadensis	1.71 ± .15	5	10.00 ± 1.47	5
	S. juncea	.92 ± .19	5	12.00 ± .89	5
16-18	S. canadensis	1.04 ± .15	6	9.33 ± 1.49	6
	S. juncea	1.14 ± .13	5	10.00 ± .35	5
18-20	S. candensis	.74 ± .08	3	5.83 ± 1.09	3
	S. juncea	1.21	1	10.00	1

APPENDIX H

Greenhouse Measurements of Stomatal Conductance and Leaf Water Potential: Transplants, Sampling Date 2, June 28, 1979. Data represent means from two hour intervals ± 1 standard error.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	N	Leaf Water Potential (bars)	N
8-10	S. canadensis	.96	1	1.50	1
10-12	S. canadensis	.88 ± .09	6	6.66 ± 1.06	6
	S. juncea	.94 ± .14	6	8.91 ± 1.48	6
12-14	S. canadensis	1.03 ± .09	7	8.00 ± .44	7
	S. juncea	.83 ± .09	2	9.25 ± 1.24	2
14-16	S. canadensis	1.75 ± .57	3	9.66 ± 1.16	3
	S. juncea	1.09 ± .08	4	9.50 ± 1.20	4
16-18	S. canadensis	.88 ± .14	4	8.75 ± 1.12	4
	S. juncea	.86 ± .14	6	8.50 ± 1.15	6
18-20	S. canadensis	1.03 ± .43	3	5.16 ± 1.29	3
	S. juncea	.50 ± .14	3	4.50 ± .49	3

APPENDIX I

Greenhouse Measurements of Stomatal Conductance and Leaf Water Potential: Transplants, Sampling Date 3, August 2, 1979. Data represent means from two hour intervals ± 1 sandard error.

Time of day	Species/Stage	Stomatal Conductance ($^{cm}/_{sec}$)	N	Leaf Water Potential (bars)	N
8-10	S. canadensis	1.15 ± .60	5	5.70 ± .69	5
	S. juncea	.55 ± .04	3	5.50 ± 2.02	3
10-12	S. canadensis	1.78 ± .37	10	7.95 ± .81	11
	S. juncea	1.03 ± .43	3	6.50 ± 3.01	3
12-14	S. canadensis	2.80 ± 1.34	2	10.50 ± .28	3
	S. juncea	.67 ± .17	3	8.00 ± 3.60	3
14-16	S. canadensis	.69 ± .19	5	10.80 ± 1.14	5
	S. juncea	.86 ± .17	11	11.59 ± 1.30	11

APPENDIX J

Greenhouse Measurements of Stomatal Conductance and Leaf Water Potential: Transplants, Sampling Date 4, September 14, 1979. Data represent means of two hour intervals ± 1 standard error.

Time of day	Species/Stage	Stomatal Conductance ($^{cm}/_{sec}$)	N	Leaf Water Potential (bars)	N
8-10	S. canadensis	.33 ± .088	5	6.20 ± .97	5
	S. juncea	.78	1	5.00	1
10-12	S. canadensis	.32 ± .054	5	9.30 ± 1.29	5
	S. juncea	.50 ± .068	6	6.83 ± 1.55	6
12-14	S. canadensis	.17 ± .040	4	9.12 ± 1.88	4
	S. juncea	.61 ± .137	3	5.00 ± .86	3
14-16	S. canadensis	.43 ± .106	5	7.94 ± 1.36	5
	S. juncea	.50 ± .074	9	2.95 ± .49	9
16-18	S. canadensis	.25 ± .044	2	12.50 ± 5.09	2
	S. juncea	.44 ± .049	4	2.15 ± .56	4

APPENDIX K

Greenhouse Measurements of Stomatal Conductance and Leaf Water Potential: Transplants, Daily Means ± 1 Standard Error From All Four Sampling Dates.

Sampling Date	Species	Stomatal Conductance ($^{cm}/_{sec}$)	N	Leaf water Potential (bars)	N
June 16, 1979	S. canadensis	1.41 ± .18	22	7.25 ± .77	24
	S. juncea	1.29 ± .10	24	10.51 ± .40	24
June 28, 1979	S. canadensis	1.05 ± .10	24	7.37 ± .52	24
	S. juncea	.87 ± .06	24	8.31 ± .58	24
Aug. 2, 1979	S. canadensis	1.39 ± .26	22	8.39 ± .58	24
	S. juncea	.96 ± .15	24	9.38 ± .94	24
Sept. 14, 1979	S. canadensis	.31 ± .03	24	8.54 ± .67	24
	S. juncea	.52 ± .03	24	4.35 ± .55	24

APPENDIX L

Stomatal Number and Stomatal Conductances From the Greenhouse Transplants on Sampling Date 1, June 16, 1979. The number of stomata in 20, .066 mm^2, fields of view were averaged for a mean surface value (stomata per mm^2). Stomatal conductances are given in cm sec^{-1}. Adax. = adaxial, Abax. = abaxial.

Greenhouse Soil Moisture Level

S. juncea genotype		3 (dry)		6		9		11 (wet)	
		Adax.	Abax.	Adax.	Abax.	Adax.	Abax.	Adax.	Abax.
1	number	89.0	209.9	62.2	137.1	37.1	78.7	9.0	56.8
	conductance	.62	.77	.60	2.47	.25	.51	.16	.91
2	number	98.4	80.2	--	--	91.6	151.5	39.3	75.7
	conductance	.56	1.05	--	--	.95	1.24	.43	.58
3	number	--	--	56.8	120.4	67.4	227.2	--	--
	conductance	--	--	.56	.95	.21	.21	--	--
4	number	125.7	171.9	82.5	123.4	53.7	143.9	36.3	63.6
	conductance	.44	.77	.54	1.34	.50	1.01	.39	.70
5	number	21.2	52.2	34.8	99.9	26.5	73.4	34.8	63.6
	conductance	.26	.79	.22	.73	.05	.51	.24	.62
6	number	--	--	--	--	73.4	129.5	118.9	200.7
	conductance	--	--	--	--	.53	.78	.45	.61

APPENDIX L (Continued)

Greenhouse Soil Moisture Level

S. canadensis genotype		3 (dry)		6		9		11 (wet)	
		Adax.	Abax.	Adax.	Abax.	Adax.	Abax.	Adax.	Abax.
7	number	--	--	24.9	173.4	24.7	225.5	7.5	242.0
	conductance	--	--	.13	.79	.19	3.38	.03	.59
8	number	0.0	133.3	17.4	215.1	34.0	219.6	2.1	158.3
	conductance	.09	1.68	.13	.61	.21	1.56	.05	2.03
9	number	15.9	216.6	0.7	250.7	2.2	118.9	0.0	297.6
	conductance	.17	.97	.04	.81	.01	.69	.02	.95
10	number	3.7	181.8	3.5	91.9	0.0	189.3	2.2	112.8
	conductance	.07	1.64	.06	1.09	.03	max.	.05	1.08
11	number	2.2	173.4	25.4	229.0	.7	128.0	2.2	146.9
	conductance	.05	1.37	.23	2.39	.03	.81	.02	.75
12	number	11.3	263.0	3.0	170.4	0.0	208.5	0.0	146.9
	conductance	.09	max.	.03	1.91	.03	2.77	.04	1.96

APPENDIX M

Greenhouse Diel Measurements of Stomatal Conductance and Leaf Water Potential, August 24, 1979. Measurements were made on one S.canadensis transplant which was bolting, one S. juncea transplant which was bolting and two transplants of S. juncea rosettes which were sampled from alternately. All four transplants were growing on soil moisture levels 5 or 6. Maximum conductance values were the result of low or negative resistance measurements.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	Leaf water Potential (bars)
23-24	S. canadensis	.37	6.0
	S. juncea, flowering	1.57	9.0
	S. juncea, rosette	.05	9.5
5-6	S. canadensis	.19	3.5
	S. juncea, flowering	.97	2.0
	S. juncea, rosette	.37	4.5
7-8	S. canadensis	.26	3.5
	S. juncea, flowering	.72	10.0
	S. juncea, rosette	.41	2.5
9-10	S. canadensis	.55	6.0
	S. juncea, flowering	1.83	13.5
	S. juncea, rosette	.35	5.0

APPENDIX M (Continued)

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	Leaf water Potential (bars)
11-12	S. canadensis	.40	5.0
	S. juncea, flowering	.30	12.0
	S. juncea, rosette	.70	4.5
13-14	S. canadensis	.21	5.0
	S. juncea, flowering	1.25	9.5
	S. juncea, rosette	.50	6.0
15-16	S. canadensis	.34	8.0
	S. juncea, flowering	max.	11.5
	S. juncea, rosette	.85	8.5
17-18	S. canadensis	.42	6.0
	S. juncea, flowering	max.	15.0
	S. juncea, rosette	.84	8.5
19-20	S. canadensis	.20	5.5
	S. juncea, flowering	2.12	11.0
	S. juncea, rosette	.34	6.5
21-22	S. canadensis	.16	4.0
	S. juncea, flowering	.72	5.0
	S. juncea, rosette	.36	4.0

APPENDIX N

Analysis of Variance: Greenhouse Diel Measurements of Stomatal Conductances and Leaf Potential of Transplants.

Leaf Water Potentials (bars)

S. canadensis	*S. juncea*, flowering	*S. juncea*, rosette
$n = 10$	$n = 10$	$n = 10$
$\overline{X} = 5.25$	$\overline{X} = 9.85$	$\overline{X} = 5.35$
S.D. = 1.37	S.D. = 3.86	S.D. = 2.53
$\Sigma X_i^2 = 292.75$	$\Sigma X_j^2 = 1104.75$	$\Sigma X_k^2 = 344.25$
$\Sigma X_i = 52.50$	$\Sigma X_j = 98.5$	$\Sigma X_k = 53.50$

Treatments = 3
Replicates = 10

$$\text{Correction term} = \frac{(52.5 + 98.5 + 53.5)^2}{30} = 1394$$

Total SS = 292.75 + 1104.75 + 344.25 - 1394 = 347.75

$$\text{Treatment SS} = \frac{(52.5^2 + 98.5^2 + 53.5^2)}{10} - 1394 = 138.07$$

Error SS = 347.75 - 138.07 = 209.68

Source of variance	df	MS	F	
treatment	2	69	8.89	P = .01
error	27	7.76		
total	29			

APPENDIX N (Continued)

Stomatal Conductances (cm sec^{-1})

S. canadensis	*S. juncea*, flowering	*S. juncea*, rosette
$n = 10$	$n = 8$	$n = 10$
$\bar{X} = .31$	$\bar{X} = 1.18$	$\bar{X} = .58$
S.D. = .12	S.D. = .62	S.D. = .45
$\Sigma X_i^2 = 1.10$	$\Sigma X_j^2 = 13.93$	$\Sigma X_k^2 = 5.26$
$\Sigma X_i = 3.10$	$\Sigma X_j = 9.48$	$\Sigma X_k = 5.83$

Treatment = 3
Replicates = 10

$$\text{Correction term} = \frac{(3.10 + 9.48 + 5.83)^2}{30} = 11.29$$

Total SS = 1.10 + 13.93 + 5.26 - 11.29 = 9.00

$$\text{Treatment SS} = \frac{3.10^2 + 9.48^2 + 5.83^2}{10} - 11.29 = 2.05$$

Error SS = 9 - 2.05 = 6.95

Source of variance	df	MS	F	
treatment	2	1.02	3.96	n.s.
error	27	.25		
total	29			

APPENDIX O

Greenhouse Measurements of Conductance and Leaf Water Potential: Seedlings, August 24, 1979. Data represent means of two hour intervals ± 1 standard error.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	N	Leaf water Potential (bars)	N
9-11	S. canadensis	1.21 ± .26	4	5.00 ± .35	4
	S. juncea	1.17 ± .12	5	6.60 ± .53	5
11-13	S. canadensis	1.12 ± .22	6	8.91 ± .37	6
	S. juncea	1.21 ± .19	5	9.30 ± .33	5
14-16	S. canadensis	.88 ± .16	5	8.60 ± 1.05	5
	S. juncea	.91 ± .20	5	10.00 ± .64	5
17-18	S. canadensis	.44 ± .07	5	7.60 ± .96	5
	S. juncea	.82 ± .08	5	9.40 ± .65	5

APPENDIX P

Analysis of Variance: Greenhouse Seedling Measurements of Stomatal Conductance and Leaf Water Potential, August 24, 1979.

Leaf Water Potential (bars)

S. juncea	*S. canadensis*
$n = 20$	$n = 20$
$\overline{X} = 8.825$	$\overline{X} = 7.725$
S.D. = 1.77	S.D. = 2.22
$\Sigma X_i^2 = 1617.25$	$\Sigma X_j^2 = 1287.75$
$\Sigma X_i = 176.5$	$\Sigma X_j = 154.5$

Treatments = 2
Replicates = 20

$$\text{Correction term} = \frac{(176.5 + 154.5)^2}{(2)(20)} = 2739.025$$

Total SS = (1617.25 + 1287.75) - 2739.025 = 166

$$\text{Treatment SS} = \frac{(1765)^2 + (154.5)^2}{20} - 2739.025 = 12.1$$

Error SS = 166 - 12.1 = 53.9

Source of variance	df	MS	F	
treatment	1	12.1	2.987	n.s.
error	38	4.05		
total	39			

APPENDIX P (Continued)

Stomatal Conductance (cm sec^{-1})

S. juncea	S. canadensis
$n = 20$	$n = 20$
$\bar{X} = 1.03$	$\bar{X} = .91$
S.D. = .37	S.D. = .50
$\Sigma X_i^2 = 23.98$	$\Sigma X_j^2 = 21.44$
$\Sigma X_i = 20.64$	$\Sigma X_j = 18.25$

Treatments = 2
Replicates = 20

$$\text{Correction term} = \frac{(20.64 + 18.25)^2}{(2)(20)} = 37.81$$

Total SS = 23.986 + 21.444 - 37.81 = 7.62

$$\text{Treatment SS} = \frac{(20.64)^2 + (18.25)^2}{20} - 37.81 = .143$$

Error SS = 7.62 - .143 = 7.47

Source of variance	df	MS	F	
treatment	1	.143	.727	n.s.
error	38	.196		
total	39			

APPENDIX Q

Greenhouse Measurements of Stomatal Conductance and Leaf Water Potential: Seedlings, September 18, 1979. Data represent means of two hour intervals.

Time of day	Species/Stage	Stomatal Conductance (cm/sec)	N	Leaf water Potential (bars)	N
9-11	S. canadensis	.586 ± .09	5	3.68 ± .80	5
	S. juncea	.776 ± .10	6	5.93 ± .64	6
11-13	S. canadensis	.630 ± .16	4	9.65 ± 1.45	4
	S. juncea	.793 ± .07	3	10.73 ± .63	3
13-15	S. canadensis	.586 ± .06	6	9.56 ± .75	6
	S. juncea	.715 ± .08	6	10.85 ± .37	6
15-17	S. canadensis	.540 ± .05	5	9.32 ± .46	5
	S. juncea	.582 ± .06	5	11.24 ± .49	5
17-19	S. canadensis	.580 ± .26	4	4.55 ± .10	4
	S. juncea	.465 ± .08	4	7.75 ± .77	4

APPENDIX R

Analysis of Variance: Greenhouse Seedling Measurements of Stomatal Conductance and Leaf Water Potential, September 18, 1979.

Leaf Water Potential

S. juncea	S. canadensis
$n = 24$	$n = 24$
$\bar{X} = 9.17$	$\bar{X} = 7.46$
S.D. = 2.53	S.D. - 3.24
$\Sigma X_i^2 = 2166.23$	$\Sigma X_j^2 = 1580.36$
$\Sigma X_i = 220.1$	$\Sigma X_j = 179.2$

Treatments = 2
Replicates = 24

$$\text{Correction term} = \frac{(220.1 + 179.2)^2}{48} = 3321.67$$

$$\text{Total SS} = 2166.23 + 1580.36 - 3321.67 = 424.92$$

$$\text{Treatment SS} = \frac{(\Sigma Xi)^2+(\Sigma Xj)^2}{r} - C = \frac{(220.1)^2+(179.2)^2}{24} - 3321.67 = 34.85$$

Error SS = 424.92 - 34.85 = 390.07

Source of variance	df	MS	F	
treatment	1	34.85	4.10	n.s.
error	46	8.47		
total	47			

APPENDIX R (Continued)

Stomatal Conductance

S. juncea	S. canadensis
$n = 24$	$n = 24$
$\bar{X} = .67$	$\bar{X} = .58$
S.D. = .22	S.D. = 26
$\Sigma X_i^2 = 11.92$	$\Sigma X_j^2 = 9.76$
$\Sigma X_i = 16.10$	$\Sigma X_j = 13.99$

Treatments = 2
Replicates = 24

$$\text{Correction term} = \frac{(16.10 + 13.99)^2}{(2)(24)} = 18.86$$

Total SS = 11.92 + 9.76 - 18.86 = 2.82

$$\text{Treatment SS} = \frac{(16.10)^2 + (13.99)^2}{24} - 18.86 = .09$$

Error SS = 2.82 - .095 = 2.72

Source of variance	df	MS	F	
treatment	1	.095	1.610	n.s.
error	46	.059		
total	47			

APPENDIX S

Assimilation Rates and Percent of Maximum Assimilation Rate for Leaves of *S. canadensis* and *S. juncea* at Different Light Intensities.

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Nov. 27, 1979	*S. canadensis*	1	0	-3.49	-20.0
			62	2.23	12.7
			200	11.90	68.2
			400	16.30	93.5
			780	17.43	100.0
	S. canadensis	2	0	-2.04	-16.1
			62	3.34	26.5
			200	12.60	100.0
			400	9.98	79.2
			780	7.34	58.2
	S. juncea	1	0	-1.26	-7.8
			62	2.47	15.4
			200	10.53	65.6
			400	14.00	87.3
			780	16.03	100.0
	S. juncea	2	0	-2.47	-37.1
			62	1.68	25.3
			200	5.53	83.2
			400	6.64	100.0
			780	6.35	95.6

APPENDIX S (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Dec. 3, 1979	S. canadensis	3	0	-.60	-3.9
			65	3.62	23.8
			218	10.93	71.9
			794	15.20	100.0
	S. canadensis	4	0	-.79	-7.9
			65	1.99	19.7
			218	7.08	70.3
			794	10.06	100.0
	S. juncea	3	0	-2.73	-28.5
			65	1.46	15.0
			218	7.40	76.2
			794	9.71	100.0
	S. juncea	4	0	-3.63	-28.0
			65	1.37	10.5
			218	9.33	72.1
			794	12.93	100.0

APPENDIX S (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Mar. 21, 1979	S. canadensis	5	0	-	-
			46	2.01	15.2
			200	10.65	80.6
			385	12.26	92.8
			550	13.20	100.0
	S. juncea	5	0	-.96	-6.1
			46	3.75	23.9
			200	15.63	100.0
			385	14.50	92.7
			550	13.43	85.9
	S. juncea	6	0	-.76	-4.5
			46	2.90	17.4
			200	12.30	73.8
			385	15.30	91.8
			550	16.66	100.0

APPENDIX S (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Mar. 23, 1979 a.m.	S. canadensis	6	0	-.32	-1.8
			42	3.14	18.6
			187	14.30	84.8
			560	16.86	100.0
	S. canadensis	7	0	-.64	06.4
			42	1.65	16.5
			187	8.18	81.8
			560	9.99	100.0
	S. juncea	7	0	-.34	-2.94
			42	1.44	12.4
			187	9.66	83.5
			560	11.56	100.0
	S. juncea	8	0	-1.50	-8.7
			42	2.83	16.5
			187	13.60	79.7
			560	17.06	100.0

APPENDIX S (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Mar. 23, 1979 p.m.	S. canadensis	8	0	-.32	-2.3
			47	2.43	17.5
			227	12.06	87.2
			613	13.83	100.0
	S. canadensis	9	0	-.61	-6.5
			47	1.58	17.0
			227	8.05	86.9
			613	9.26	100.0
	S. juncea	9	0	-1.09	-7.4
			47	3.05	20.8
			227	13.13	89.5
			613	14.66	100.0
	S. juncea	10	0	-.78	-6.5
			47	2.01	16.7
			227	10.05	83.7
			613	12.00	100.0

APPENDIX T

Stomatal Conductances and Percent of Maximum Stomatal Conductance for Leaves of *S. canadensis* and *S. juncea* at Different Light Intensities.

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Nov. 27, 1979	*S. canadensis*	1	0	21.4	54.5
			62	25.3	64.5
			200	35.9	91.5
			400	38.4	97.9
			780	39.2	100.0
	S. canadensis	2	0	17.6	70.9
			62	23.0	70.9
			200	24.8	100.0
			400	12.1	48.7
			780	8.4	33.9
	S. juncea	1	0	8.8	16.6
			62	16.2	30.5
			200	43.2	81.3
			400	46.6	87.7
			780	53.1	100.0
	S. juncea	2	0	17.9	86.8
			62	20.6	100.0
			200	15.1	73.3
			400	13.9	67.4
			780	9.7	47.2

APPENDIX T (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Dec. 3, 1979	S. canadensis	3	0	13.0	36.7
			65	14.3	40.3
			218	19.3	54.5
			794	35.4	100.0
	S. canadensis	4	0	4.3	23.2
			65	4.7	24.8
			218	9.6	50.7
			794	18.9	100.0
	S. juncea	3	0	18.0	56.7
			65	18.5	58.3
			218	20.5	64.6
			794	31.7	100.0
	S. juncea	4	0	31.0	59.6
			65	32.4	62.3
			218	39.4	75.7
			794	52.0	100.0
Mar. 21, 1979	S. canadensis	5	0	-	-
			46	20.3	74.6
			200	23.1	84.9
			385	25.1	92.2
			550	27.2	100.0

APPENDIX T (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Mar. 21, 1979	S. juncea	5	0	12.7	32.9
			46	38.6	100.0
			200	35.4	91.7
			385	16.5	47.7
			550	12.6	32.6
	S. juncea	6	0	4.9	12.9
			46	17.2	45.3
			200	32.8	86.5
			385	36.7	96.8
			550	37.9	100.0
Mar. 23, 1979 a.m.	S. canadensis	6	0	9.4	21.6
			42	19.1	43.8
			187	29.9	68.5
			560	43.6	100.0
	S. canadensis	7	0	14.1	51.8
			42	17.4	64.1
			187	25.2	92.8
			560	27.2	100.0

APPENDIX T (Continued)

Date	Species	Leaf	Light (w m^{-2})	Assimilation (micromoles CO_2 m^{-2} sec^{-1})	Percent of Maximum (per leaf)
Mar. 23, 1979 a.m.	S. juncea	8	0	10.0	21.5
			42	24.2	52.5
			187	36.2	78.0
			560	46.4	100.0
Mar. 23, 1979 p.m.	S. canadensis	8	0	3.7	11.9
			47	17.6	56.4
			227	26.7	85.5
			613	31.2	100.0
	S. canadensis	9	0	5.3	14.7
			47	22.3	61.4
			227	31.8	87.6
			613	36.3	100.0
	S. juncea	9	0	9.7	23.7
			47	24.8	60.3
			227	41.1	100.0
			613	36.7	89.2
	S. juncea	10	0	2.7	10.1
			47	8.7	32.8
			227	19.1	72.8
			613	26.5	100.0

APPENDIX U

Water Use Efficiency and Percent of Maximum Water Use Efficiency for Leaves of *S. canadensis* and *S. juncea* at Different Light Intensities. WUE was calculated as Assimilation/Evaporation.

Date	Species	Leaf	Light (w m^{-2})	Water Use Efficiency (micromoles CO_2 $millimoles^{-1}$ H_2O)	Percent of Maximum (per leaf)
Nov. 27, 1979	*S. canadensis*	1	0	-4.63	-141.8
			62	.91	27.7
			200	3.28	100.0
			400	2.79	85.0
			780	2.74	83.5
	S. canadensis	2	0	-2.02	-37.2
			62	1.32	24.3
			200	4.12	76.0
			400	5.42	100.0
			780	3.86	71.2
	S. juncea	1	0	-2.96	-113.8
			62	.77	29.6
			200	2.37	91.1
			400	2.60	100.0
			780	2.01	77.3
	S. juncea	2	0	-2.10	-65.2
			62	.70	21.7
			200	2.88	89.4
			400	3.22	100.0
			780	2.99	92.8

APPENDIX U (Continued)

Date	Species	Leaf	Light (w m^{-2})	Water Use Efficiency (micromoles CO_2 millimoles^{-1} H_2O)	Percent of Maximum (per leaf)
Dec. 3, 1979	S. canadensis	3	0	-.52	-15.4
			65	2.09	62.2
			218	3.36	100.0
			794	1.74	51.7
	S. canadensis	4	0	-1.25	-35.2
			65	1.99	56.0
			218	3.55	100.0
			794	1.87	52.6
	S. juncea	3	0	-1.69	-72.8
			65	.73	31.4
			218	2.32	100.0
			794	2.27	97.8
	S. juncea	4	0	-1.35	-64.9
			65	.39	18.7
			218	1.91	91.8
			794	2.08	100.0
Mar. 21, 1979	S. canadensis	5	0	-	-
			46	.90	21.2
			200	4.23	100.0
			385	3.99	94.3
			550	3.61	85.3

APPENDIX U (Continued)

Date	Species	Leaf	Light (w m^{-2})	Water Use Efficiency (micromoles CO_2 $millimoles^{-1}$ H_2O)	Percent of Maximum (per leaf)
Mar. 21, 1979	S. juncea	5	0	-.71	-12.1
			46	1.11	18.9
			200	4.29	73.2
			385	5.86	100.0
			550	5.83	99.4
	S. juncea	6	0	-1.35	-36.2
			46	1.65	44.3
			200	3.72	100.0
			385	3.65	98.1
			550	3.36	90.3
Mar. 23, 1979 a.m.	S. canadensis	6	0	-.74	-16.8
			42	1.42	32.3
			187	4.39	100.0
			560	3.24	73.8
	S. canadensis	7	0	-1.96	-50.3
			42	1.66	42.6
			187	3.89	100.0
			560	2.68	68.8
	S. juncea	7	0	-1.03	-30.8
			42	1.28	38.3
			187	3.34	100.0
			560	2.99	89.5

APPENDIX U (Continued)

Date	Species	Leaf	Light (w m^{-2})	Water Use Efficiency (micromoles CO_2 millimoles^{-1} H_2O)	Percent of Maximum (per leaf)
Mar. 23, 1979 a.m.	S. juncea	8	0	-1.31	-40.8
			42	.96	29.9
			187	3.21	100.0
			560	2.59	80.6
Mar. 23, 1979 p.m.	S. canadensis	8	0	-.31	-6.5
			47	1.68	35.2
			227	4.76	100.0
			613	3.13	65.7
	S. canadensis	9	0	-.47	-14.2
			47	1.00	30.3
			227	3.30	100.0
			613	2.86	86.6
	S. juncea	9	0	-.68	-19.7
			47	.97	28.1
			227	3.45	100.0
			613	2.54	73.6
	S. juncea	10	0	-1.39	-36.7
			47	1.24	32.8
			227	3.78	100.0
			613	2.99	79.1