STOMATAL RESPONSE OF *CAREX AQUATILIS*
TO
CLIMATE CONDITIONS
IN A
SUBARCTIC COASTAL WETLAND
DURING THE GROWING SEASON

BY

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Abstract:

Plants can control water loss through their stomata in response to changing environmental conditions. Some research has been done on predicting stomatal resistance from climate variables such as solar radiation intensity, temperature, and vapour pressure deficit, but the factors involved are numerous and complex. Information on evapotranspiration from non-cultivated vegetation under field conditions is relatively scarce. This study was carried out in a subarctic coastal wetland on James Bay, an area for which little data exists. Leaf resistance measurements were collected in the field with a diffusion porometer as the 1988 growing season reached its peak. Meteorological data were also recorded. The main species examined was *Carex aquatilis* , a common sedge with a circumpolar distribution. As has been previously found, field resistances were lower than those reported for greenhouse-grown specimens. Attempts to derive a multivariate regression model to predict leaf resistances had a maximum explained variance under 40%. However, Principal Components Analysis suggested that cool, sunny, low-VPD conditions tend to accompany low leaf resistances. An increase in leaf resistance occurs when solar radiation intensities are low, or when the air is warm and dry. In addition, *Carex aquatilis* from drier areas showed less growth, and generally higher leaf resistances, than plants growing in saturated soils. Since climate models predict higher temperatures and lower soil moisture for the study area, due to carbon dioxide-induced warming, higher stomatal resistances could result. If these changes are severe enough, primary production could be reduced in the subarctic wetlands. Through the food chain, this could possibly affect species important to the economy and ecology of northern areas.

Keywords: stomatal resistance, evapotranspiration, James Bay, subarctic wetland, *Carex aquatilis*, Principal Components Analysis.

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Table of Contents

List of Figures and Tables:

List of Figures and Tables, contd.

Introduction:

The importance of plant stomata in regulating transpiration has been recognized for at least a century (Jarvis and McNaughton 1986). Studies have been done on the process of gas diffusion through isolated pores, single leaves, whole plants, and more recently, vegetation canopies. The pathways taken by water and carbon dioxide after they enter the soil-plant-air system have been examined (Oke 1978, chap. 4; Simpson 1981), and differences in the design, efficiency, size, arrangement, and frequency of the stomata have been noted, among as well as within various species (Korner, Scheel, and Bauer 1979; Jones 1983; Jarvis and McNaughton 1986; Standley 1986). There are two basic ways of approaching the study of stomatal resistance to the free passage of water vapour from the leaf to the atmosphere (Jarvis and McNaughton 1986). Plant physiologists and ecologists tend to focus on the water relations of groups of plants (either taxonomically related, or associated with each other in certain habitats) or individual species. Extensive laboratory work under controlled conditions has played a crucial role in developing and refining theories on the movement of water and gases through plants (Jarvis and McNaughton 1986).

In contrast, the climatological or meteorological approach considers the weather to be the most important influence on plant transpiration through the stomata, given that the plant's roots have access to an adequate supply of water (Jarvis and McNaughton

1986). The atmospheric conditions which govern evapotranspiration are regarded as being independent of the exact vegetation type, and the morphology and physiology of particular species. Climatologists are not as interested in how single leaves and individual plants respond to changes in temperature, humidity, and light intensity. Rather, they are concerned with how particular surfaces behave, with respect to the water and energy balance. Since transpiration releases water into the atmosphere in gaseous form, vegetation is a source of not only moisture, but energy as well (i.e. latent heat of vapourization, which is released when the vapour condenses).

Beginning with Thornthwaite in1948, and continuing on through the work of Penman, Turc, Monteith, Priestly and Taylor, and others, many formulae have been used to estimate evapotranspiration using only meteorological variables, without incorporating differences in species characteristics such as stomatal frequency and distribution (Jarvis and McNaughton 1986). It can readily be argued that the type of plants which make up the ground cover in a particular location (and their state of health, and maturity) cannot be ignored, if one desires a thorough understanding of canopy-atmosphere interactions under natural conditions. Jarvis and McNaughton (1986) observe that potential evaporation values derived from climatological equations are largely successful, providing that the vegetation is not suffering from water stress. This last qualification implies that care should be taken when applying these formulae since most vegetation, whether natural or cultivated, experiences periods of low water availability during the year. Wetlands are no exception.

In recent years, some attempts have been made to construct evaporation models with specific terms for canopy and stomatal resistance. Various authors have experimented with the Penman-Monteith combination equation (Monteith, cited in Lafleur and Rouse 1988; Jarvis and McNaughton 1986) and other formulae (Thom (1972), cited in Bailey and Davies 1981; Stewart and Thom, and Thom (1975), both cited in Lafleur and Rouse 1988; and Jarvis, cited in Lafleur 1988). Multiple regression techniques and boundary line analysis of dominant weather variables have also been explored, with some success (Lafleur 1988).

Up to now, most studies of stomatal resistance have been of the ecological/physiological variety. Laboratory experiments under controlled conditions outnumber field observations by a considerable margin, although Lafleur (1988) notes that field work has been increasing in the last two decades. It seems likely that this trend is due in least in part to improvements in technology which have allowed the development of reliable equipment which can be used in the field. Even today, however, research into plant physiology and biochemistry requires special facilities and controlled conditions which restrict this type of work to laboratories (Lafleur 1988).

It is important to realize that these two lines of research are not mutually exclusive. Field studies may be used to test theories developed from laboratory experiments, and can offer new insights into the complex processes at work in vegetation canopies. Jarvis and McNaughton (1986) believe that it is highly desirable to observe the activity of unenclosed plants growing under natural conditions, since there are problems inherent in extrapolating theories from single pores up to leaves and entire canopies. They conclude that researchers must always be mindful of the concept of scale, regardless of whether they use the physiological or the meteorological approach. In other words, we cannot assume that an individual bean plant in a pot, or a small clump of plants in a suburban garden, will be subject to the same environmental conditions as a 40- hectare bean field. It has been well-documented that greenhouse-grown plants, which are often used in water-relations studies, tend to exhibit higher minimum resistances than wild specimens, for reasons which have not yet been adequately explained (Korner, Scheel, and Bauer 1979); Lafleur 1988). There can also be a substantial variation in resistance values, depending on the measurement device used (Korner, Scheel, and Bauer 1979). Unfortunately, it is not always possible to find comparative values, since the data base of leaf resistances is still relatively small (only 250 or so plant species and cultivars, as assembled by Korner, Scheel, and Bauer in 1979). More work has been done on agricultural crops and tree types used in forestry than on species with little perceived economic value from wetlands (Lafleur 1988), deserts, and alpine environments. Logistics may also contribute to this imbalance, since it is comparatively easier to carry out research on cultivated land than it is to set up measurement programmes in remote, relatively undisturbed wilderness where the terrain may be quite rugged or boggy. However, there is an obvious need to obtain information from natural areas, since large portions of the Earth's surface remain dominated by woodland, grassland, taiga, and tundra. The vegetation component plays an essential role in the water balance, ecology, and human economies of these regions.

Study Site:

Field research was carried out at Ekwan Point, located at 53'17"N, 82'07"W on the western shore of James Bay, 20 km north of the mouth of the Ekwan River (Fig. 1). The study area is quite flat, with a slope of about 2 m per km. Beach soils are composed of silt with deposits of sand and gravel at depths of 30 cm or more. The coastline is emergent, and its development may be traced through a well-developed series of beach ridges which have been built up parallel to the coast, as the land experiences isostatic rebound. Similar shorelines occur throughout the James Bay and Hudson Bay Lowlands, north of Churchill, Manitoba, and south as far as the tip of James Bay (Lafleur 1988). Glooschenko (1982) describes these coastal wetlands as "fairly young, dynamic ecosystems" (p. 56) which are often less than 300 years old, having been created by rapid isostatic uplift. Glooschenko cites "salinity, drainage, and time" as being the major factors influencing the vegetation patterns in such areas (p. 57). Fens often develop in poorly-drained depressions, while the beach ridges and other upland areas may be colonized by shrubs, trees, and lichens.

The vegetation in the vicinity of Ekwan Point is a mixture of tundra, taiga, and coastal species. Both the southern limit of continuous permafrost and the northern limit of forest growth run southeast across the continent, bend to follow the shore of Hudson Bay, and appear to converge at about 53°N on the western side of James Bay (Rouse, Hardill, and Lafleur 1987), the approximate location of Ekwan Point. These same authors note that in Hudson Bay as well as in James Bay, species found in arctic and subarctic wetlands dominate the vegetation for 2 km or more inland from the shoreline.

Distinct vegetation zones were evident at Ekwan Point. The area nearest to the Bay was dominated by *Puccinellia phryganodes*. About 200 m further inland, *Potentilla egedii* and *Carex subspathacea* became common. The next zone was salt pan, barren of plants except for halophytes such as *Salicornia europaea*. The tidal surge observed at the beginning of August sent salt water up as far as a fourth zone, where taller grasses (*Calamagrostis neglecta, C. canadensis*, and *Hordeum jubatum*) emerged. Farther inland was a damp area underlain by mosses, with occasional stands of moisture-loving species such as *Carex aquatilis* . A thin belt of shrubs (*Salix* spp., with some *Betula glandulosa*) up to 1.5 -2.0 m in height, occurred at about 800 m inland from the high tide mark. Between this zone and the first forested beach ridge, there was a large fen dominated by *Carex aquatilis* and occasional *Salix* . Other species found in this area were *Caltha palustris* (marsh marigold), *Petasites sagittatus*, *Eriophorum* spp., *Potentilla palustris*, and *Menyanthes trifoliata* (bogbean). The vegetation was especially lush around a small pond which shrank as the summer progressed, but remained full of standing water through the growing season.

The main climate research site was set up in the open coastal area, about 200 m shoreward from the shrub line (Fig. 2a). Leaf resistance data were collected in two locations: the "meadow" site (Fig. 2c), just behind the first band of *Salix* shrubs (200 m west of the main site) and the "pond" site (Fig. 2d), at the verge of the pond, some 250 m northwest of the "meadow" site. Most of the measurements of leaf resistance apply to *Carex aquatilis*, although some readings were obtained from *Menyanthes trifoliata* growing at the pond site, for comparative purposes. This was only possible later in July, once the pond level had dropped sufficiently to allow measurements to be made without danger of immersing the equipment in water.

It was assumed that the soil at the pond site was completely saturated through the entire observational period. This was not the case at the meadow site. Water table measurements taken in the shrub zone indicated that the water table dropped steadily from the surface to a depth of more than 0.5 m. This occurred because there was no significant precipitation from late June until the fourth week of July. After the first major rainstorm on 22 July, the water table rose by 30 cm in one day, and remained within 0.5 m of the surface until observations were discontinued in the first week of August.

In addition to the dry period in June and July, there was another factor which may have had some effect on the climate at the coast. Local inhabitants reported that offshore sea ice was unusually severe, and persisted in patches until the first week of July, although it had broken up long before then. Since there were no comparative data from previous years, it is impossible to say what impact, if any, the extended presence of ice on James Bay had on the coastal energy balance and vegetation growth patterns.

Methods (Measurement and Instrumentation):

Incident solar radiation, wind speed and direction, and dry and wet bulb temperatures were measured at the main climatological site, and recorded on a CR7 Campbell Scientific datalogger, in hourly averages. The scan interval was 10 seconds. Solar irradiance was measured with a black and white Eppley pyranometer mounted 1 m above the ground on a post. It was checked daily and adjusted to insure that it was horizontal. Wind speed was measured with anenometers at heights of 0.5, 1.0, 1.5, and 2.0 m above the ground, on a separate wind mast. Wind direction was determined with a wind vane on top of the main mast. The wet-dry psychrometers were mounted at heights of 0.5, 1.0, 1.5, and 2.0 m on the main mast (Fig. 2b). Each shielded psychrometer consisted of one dry thermocouple and one which was encased in a saturated cotton wick, supplied from a water reservoir. The psychrometers were mounted facing east, towards James Bay, and were aspirated by battery-powered fans. On Julian Day 184, all of the anenometers and psychrometers were moved up a height of 10 cm, to compensate for the growth of the vegetation. Only the data from the highest wind and temperature sensors have been used in subsequent analysis, since it is assumed that they are the most representative of regional atmospheric conditions, and therefore applicable across a wider area. The difference between wet and dry-bulb temperatures, $T_a - T_w$, was converted into the vapour pressure deficit (VPD) with the following equation:

$$e = e^{*}_{(TW)} - \frac{C_p P}{0.622 L_v}(T_a - T_w) \qquad (1)$$

where e is the vapour pressure at dry bulb temperature, $e^{*}(T_w)$ is the saturation vapour pressure at the wet bulb temperature (obtained from the Smithsonian meteorological tables), C_p is the heat capacity of the air, P is the atmospheric pressure, and L_v is the latent heat of vapourization of water.

$$VPD = e^{*}(Ta) - e \qquad (2)$$

where VPD represents the difference between e, the actual vapour pressure, and $e^{*}(Ta)$, the maximum vapour pressure possible at the ambient air temperature (obtained from tables) (Oke 1978, chap. 2; Lafleur 1988).

A transient-type diffusion porometer (Mk Delta-T Devices, Burwell, UK) was used to measure leaf resistance (r_{leaf}). The sensing head of the instrument incorporates a narrow cup containing a thin film relative humidity (RH) sensor, and two thermistors to measure leaf and cup temperatures. When the sensing head is clamped to the leaf surface, the water vapour transpired through the stomata raises the relative humidity inside the cup. The instrument automatically times the increase over a set interval of RH. To improve accuracy, measurements can be repeated as many times as is necessary to achieve a stable count (usually 3 or 4 cycles). A pump fills the cup with dry air after each time count, to push the RH back down below the starting point for the timing interval. The pump then shuts off, allowing the RH inside the cup to increase again. Both pump flow rate and operating RH range can be adjusted to suit the ambient conditions. Time counts can be converted to leaf stomatal resistances by comparing them with times obtained from a calibration plate with ever-smaller holes drilled in it, which produces 6 known diffusion resistances. The manufacturer recommends that calibrations be carried out for a range of temperature and humidity conditions, since the plate diffusion resistances provided must be corrected for different temperatures.

The sedge species *Carex aquatilis* was selected because it grew in great profusion in the damp areas inland from the main climatological site, and had a leaf which, when mature, was wide enough to cover the aperture of the porometer's sensing cup. Some data were also collected from *Menyanthes trifoliata*, which was one of the few other species with a leaf area large enough for porometry. Readings on *Carex aquatilis* leaves were taken about one-third of the way down from the tip, where the leaf widened enough to accommodate the sensor, but was not so thick and rigid that it prevented the formation of a seal over the leaf's midrib, or caused the leaf to split when pressure was applied. Experimental counts were higher for the abaxial (lower) side of the leaves, indicating a higher resistance on this side, so the adaxial (upper) surfaces of *Carex aquatilis* were used to obtain the measurements. For *Menyanthes trifoliata*, the situation was reversed. The upper surfaces of the *M. trifoliata* leaves exhibited high resistances, so the undersides were used instead. Immediately before or after every porometry session, a calibration was carried out in the field using the plastic plate supplied with the instrument. This allowed the construction of a calibration curve for each porometry session, which was used to estimate the r_{leaf} values which corresponded to the time counts measured by the porometer.

Twenty individual plants, selected arbitrarily from the study patch, were sampled for every field porometry session. Leaves which were insect-damaged or in poor health were avoided. No attempt was made to use exactly the same plants each time, in case repeated insertion into the sensing head damaged the leaves and affected the results. Measurements were obtained for a range of temperature, humidity, and light conditions. The majority of the sessions were done within 3 h of solar noon, but readings were also taken in the morning and in the late afternoon and evening. No measurements were made in the darkness, because there is no photosynthetic activity at night. The porometer could not be used during rainfall or immediately afterwards, or early in the morning before the dew had evaporated, since exposure to liquid water could have damaged the sensor. For comparison of resistance values for pond and meadow sites, and for _Carex aquatilis_ and _Menyanthes trifoliata_, pairs of measurements were carried out within a few minutes of each other, to minimize the influence of atmospheric conditions.

In addition to climatological data and leaf resistances, the growth of _Carex aquatilis_ in the study area was monitored. Forty plants were marked, in 3 separate plots in the meadow site. The "open" plot represented general meadow conditions. The "grassy" plot was shielded by a layer of last year's dead grasses, _Calamagrostis neglecta_ and _Festuca_ spp.(?). Standing water persisted well into the drought period in the "wet" plot (Fig. 2c).

(At the meadow site, r_{leaf} measurements could only be made in the vicinity of the "wet" plot, since the leaves of the plants growing elsewhere were too narrow. Porometry was not carried out on individuals selected for growth monitoring.) The longest leaves of the 120 tagged and numbered specimens were measured with a tape rule every second day, through the observation season. Standing-crop dry mass estimates for both the meadow and the pond sites were taken several times, by harvesting the above-ground production of six 0.09 m^2 sample quadrats in _Carex aquatilis_ stands (two from the vicinity of each main representative plot), drying them for 48 h at 80^oC, and weighing them on a Mettler electronic balance.

In order to estimate Leaf Area Index, the unit area of photosynthesizing leaf surface per unit area of ground (Beadle 1982; Kvet et al. 1971, chap. 10), two steps were required. First, the ratio of fresh leaf area to dry mass was obtained by harvesting _Carex aquatilis_ leaves, trimming off the ends to get a hundred or more rectangular slips of a uniform length, measuring each slip in the sample at both ends to get an average width, and multiplying the sum of the average widths by the slip length, to find the sample area while the leaves were still fresh. The sample was then oven-dried and weighed, to get the dry mass term. Second, the fresh area/dry mass fraction was multiplied by an average standing crop dry mass estimate taken on the same day at the same site, to arrive at a rough estimate of the fresh leaf area per unit of ground, for a stand of

Carex aquatilis. This was done at least twice during the season for each study site.

Methods (Analysis):

The leaf resistances were averaged to obtain session means, and combined with the climate measurements for those times to create the data base for subsequent analyses. Linear correlation was used to check for relationships between r_{leaf} and individual climatic variables. Correlations between some climate variables were also calculated. An attempt was made to develop a mathematical model, using stepwise multiple regression (Minitab, Release 5.1.1.). Since the meadow site data set was too small to obtain meaningful results, only the pond site data for *Carex aquatilis* were used.

A second model was created with the same regression and stepwise commands, but this time using only the sessions from within 3 hours of solar noon. In order to test the accuracy of the models, and also check for sensitivity caused by variations in the data, four additional model equations ("Ran1", "Ran2", "Ran3", and "Ran4") were constructed, after removing 23% of the data set by random selection each time. These selected values were used to gauge the accuracy of the models, in predicting leaf resistance from the climatic variables (after Lafleur 1988).

Principal Components Analysis (PCA) was also used on the pond site data. This technique has been employed in a wide range of disciplines, from organic chemistry, metallurgy, and soil classification to ecology, anthropology, and sociology (Gauch 1982, chap. 6; Kleinbaum and Kupper, chap. 21; Flury and Riedwyl 1988, chap. 10), to search for patterns in data sets with a large number of variables which are correlated with each other and are therefore difficult to interpret individually. Previous studies examining r_{leaf} and its relationship to climate (Lafleur 1988; Lafleur and Rouse 1988; Stoner and Miller 1975; Bailey and Davies 1981) have not utilized this particular technique, although Gauch (1982, p. 234-235) cites a number of authors who have ordinated climatological and meteorological data with PCA. Enright (1984) used PCA to develop a tree ring-width chronology for white spruce (*Picea glauca*) near Schefferville, Quebec, and compares it favourably with more traditional methods for linking variations in growth rings with trends in climate.

Since the variables in the Ekwan data set were expressed in a variety of measurement units, the data first had to be standardized (Macdonald, pers. comm., 1989). This was done by calculating z-scores (number of standard deviations from the mean) for the data under each variable. An informal rule-of-thumb, which was met in this particular case, suggests that the number of data points to be analysed should be at least 3 times greater than the number of variables (Tuchscherer, pers. comm., 1989). The data were arranged in an ASCII matrix and analysed with the uncentred covariance PCA option in the MVSP statistical software package. This was first done without using the z-scores of the leaf resistances, then repeated with the z-scores of all the variables, to see whether the patterns that emerged were primarily due to the climate variables, or the r_{leaf} data. Groups of sessions that appeared to be clustered together on the all-variables PCA plot were compared using the twosample-t test (Minitab Release 5.1.1), to determine whether they were significantly different from each other. This test was also used to compare the 3 pairs of sessions for the pond and meadow sites under the same regional climate conditions, and also to compare the 2 pairs for *Carex aquatilis* and *Menyanthes trifoliata*, at the pond site.

Results and Observations:

It is evident from Fig. 3 that there can be considerable variation in growth rates for *Carex aquatilis* , within a fairly small area. For the meadow site, plants growing in the "wet" plot were significantly taller than plants in the other two plots. Growth rates for the "grassy" plot were close to the "open" plot until early July, when they diverged. By the beginning of August, the "grassy" plants had reached an average height midway between the "open" plot, where the plants were about 40 cm tall, and the "wet" plot, in which the largest plants were in excess of 55 cm. At that time, the seed heads of all of the plants were ripening, and growth had slowed. Some individuals were senescing.

Carex aquatilis at the pond site grew much faster and taller than the same species at the meadow site. For example, on 5 July, crop heights at the pond site were 60-65 cm, and the leaves were sagging. On the same day, the average height of the tagged plants in the meadow was less than 40 cm. By 14 July, the pond plants had attained a greater height than the vast majority of the meadow plants ever reached.

Table I indicates that the standing crop production of the pond site was 3 times that of the meadow. Both areas showed a crop increase until the main part of the growing season was over, which occurred by mid-July, at the pond, and late July, in the meadow. Table II shows that leaf area:mass ratios decreased slightly for both sites during the summer. Table III shows that the Leaf Area Index was 3 times higher at the pond site than it was in the meadow (Table III), since the plants were taller and more densely distributed there.

Fig. 5 shows that as mean r_{leaf} increased, the standard deviation of the resistance measurements increased linearly, with a slope of about 0.38. None of the climatological variables showed a coefficient of determination (R^2) which accounted for more than 10% of the variation of r_{leaf} (Table IV). The largest R^2 was for air temperature (9.8%), followed by leaf temperature (6.5%), VPD (5.5%), solar radiation (4.2%), and wind speed (0.6%). Correlation coefficients were negative for sunlight and wind speed, and positive for temperature and VPD (Table V). Although relationships between leaf resistance and individual climatic variables were weak, there were strong correlations between air temperature and VPD (R^2 = 71.6%), and, predictably, air temperature and leaf temperature (91.6%). Wind speed and VPD had a small positive correlation of 16.2%, possibly due to the drying effects of wind on the wet bulb sensor.

There was considerable variability in both r_{leaf} and environmental conditions during the day (Tables VIa, b). Sessions taken only 2 hours apart on the same day could display r_{leaf} values which differed by more than 600 s/m, depending on the weather,which could change from sunny to overcast, and from onshore to offshore winds in a few hours. Lafleur (1988) found that

r_{leaf} tended to be low in the morning, and to increase through the day, but this trend was not clear at Ekwan Point. A time series plot of leaf resistance and climate data (Fig. 4) suggests similarities for r_{leaf}, VPD, and temperature for the first week of measurements, but this apparent relationship disappears for the rest of the month.

The multivariate analyses all yield R^2 of less than 40% (Table VII). The regression which used only the data from within 3 hours of solar noon accounts for the most variation (36.4%). The model derived from all of the pond data for <u>Carex aquatilis</u> accounts for only 15.7%, while the four random selection models gave explained variances of between 13.1% and 24.8%. The regressions do not even agree on whether a variable is positive or negative. In addition, the residual variables left after stepwise regression differ from test to test. Logically, one might expect that either leaf temperature or air temperature would be eliminated as "redundant", given their strong correlation with each other, but this is not always the case. Flury and Riedwyl (1988, sect. 5.10) suggest that one should monitor the R^2 value as variables are being discarded, and select the last equation before a precipitous drop in this coefficent as the most reliable simplification. If this is done, the best multiple regression (R^2 = 36.1%) derived from this type of analysis may be expressed as follows:

$$r_{leaf} = 312.34 + 25.0\,(T_{leaf}) - 0.69\,(K_{down})$$

where K_{down} is incident solar radiation. VPD, which was felt to be a significant variable in other studies (Lafleur 1988; Johnson and Caldwell 1975), is eliminated as redundant.

As shown in Table VIII, the prediction accuracy of the 4 random selection models ranged from fair ("Ran 2") to poor ("Ran 4"). The models for the full data set and for the sessions within 3 hours of solar noon could not be tested in this way. Figs. 6 to 10 show the results of the principal components analyses. There are differences between the PCA plot which excluded r_{leaf} z-scores (Fig. 6) and the plot which used all of the variables (Fig. 7). In the latter case, 4 groups of sessions emerged, presumably due to the influence of the r_{leaf} term. Three of them were large enough to compare statistically (Tables IXa, b). One loose cluster, dubbed the "orange" group, was characterized by low r_{leaf}, low leaf and air temperatures, low VPD, and high solar irradiance and wind speed. The "yellow" and "green" groups both had similar high r_{leaf}. "Yellow" group had low leaf and air temperatures, and low VPD, solar radiation, and wind speed. "Green" group had high leaf and air temperatures, and high VPD, solar radiation, and wind speed.

The PCA plot of the climate variables alone (excluding leaf resistance) is also of interest. Fig. 8 shows that leaf and air temperatures and VPD are dominant on PC1 (the first principle component axis), while solar irradiance and wind are dominant on PC2. Considering that the first three variables have shown strong correlations already, this is not surprising. The reason for an apparent correlation between solar intensity and wind speed is less clear, although the R^2 for the latter two variables is small, at 10.7%. When r_{leaf} is added to the analysis (Fig. 9), it is more closely associated with PC1 than with PC2. According to the output, PC1 (temperature, VPD, and r_{leaf}) accounts for 49% of total variance in the data, while PC2 (sun and wind) accounts for 24%. Looking at the PCA plots, where distance conveys an idea of how closely variables are related, air temperature is the nearest term to r_{leaf}, with leaf temperature close behind. VPD is intermediate in distance, while solar irradiance and wind speed are the farthest away. If the plots for sessions and for variables are combined, forming what is known as a PCA "biplot" (Fig. 10), it confirms the twosample t-tests which examined the groups for statistical differences. If a best-fit line through the group is drawn through the origin, and a line perpendicular to that (nicknamed the "chop line", for lack of a more formal term) is also drawn through the origin, then it may be used to determine whether a variable has a high or a low value in a particular group. The chop line for the "orange" group separates solar radiation and wind speed (with high values) from temperature, VPD, and r_{leaf} (with low values), on the opposite side of the line. For the "green" group, all of the variables are on the same side of the "chop line" as the best-fit line, and they all have high values. For the "yellow" group, r_{leaf} alone is on the high side of the "chop line", while all of the weather variables are on the low side.

The 3 pairs of pond and meadow site porometry measurements, taken within two weeks of each other, were used to compare leaf resistances for *Carex aquatilis* growing in wet and dry environments, under the same atmospheric conditions. For 2 out of the 3 pairs (Julian Days 192 and 193), Table X shows that dry (meadow) r_{leaf} was significantly higher than it was for plants growing at the verge of the pond. The other pair of sessions (Julian Day 208) showed no significant difference at the 95% confidence level. It is possible that the differences in leaf resistance between the sites were caused by a depletion of soil moisture at the meadow site, during the long dry spell prior to 22 July (Julian Day 203). After then, r_{leaf} seemed to even out for wet and dry habitats, as the water table was replenished. When the 2 pairs of pond site sessions for mature *Carex aquatilis* and *Menyanthes trifoliata* were analysed with the twosample t-test, Table XI indicates that the r_{leaf} of the sedge was significantly higher both times, at the 95% confidence level.

Discussion and Conclusions:

Carex aquatilis is most productive in standing-water conditions. Plants in drier areas are less robust than those which are well-watered through the growing season. Prolonged surface drying can stunt vegetation development. (Since the "grassy" plot showed intermediate growth between the "open" plot and the "wet" plot, this suggests that if the ground is protected by a light-coloured, reflective canopy of last year's dead grass, it could prevent some evaporation losses and decrease moisture stress to some degree.) It is possible that this decrease in height due to drought could work in the plant's favour, since leaf size, and therefore surface transpiration area, are decreased. There are limits to tolerance, though. By the middle of July, the meadow vegetation had begun to show signs of water deprivation. This was seen in progressive browning of the leaf tips, followed by streaking and yellowing of the stem and leaves.

There is not much information on the leaf resistances of wetland vegetation. Out of the 4 wetland species studied by Lafleur, all had lower r_{leaf} than the resistance range for wetland plants suggested by Korner, Scheel, and Bauer (1979). This could be due to differences in measurement methods, and also to the fact that greenhouse-grown plants seem to have higher r_{leaf} than specimens in the field. The resistance range for *Carex aquatilis* at Ekwan Point was 120-1182 s/m, within the range of 90-1818 s/m obtained by Lafleur for *Carex paleacea*, a sedge which is similar in appearance. The previous minimum r_{leaf} reported for *Carex aquatilis* in the field is 300 s/m (Stoner and Miller 1975), 510 s/m for greenhouse specimens (Korner, Scheel, and Bauer 1979). Lafleur (1988) interpreted his maximum r_{leaf} , also measured at twilight, as the cuticular resistance when all the stomata were closed. Since Lafleur and others have found leaf resistances lower than 120 s/m, it seems that the Ekwan Point results are reliable.

Judging by the comparisions with Menyanthes trifoliata under similar weather and soil moisture conditions, r_{leaf} values can be characteristic of particular species. Plants which inhabit drier areas have an obvious need to conserve water, and this should include the ability to create very high stomatal resistances. Theoretically, plants which are largely restricted to wet areas that remain saturated through the growing season have no particular need to restrict water loss. Therefore, these species should exhibit lower resistance ranges than plants growing in drier conditions. However, if a wetland is subjected to frequent and severe droughts, species which have developed appropriate strategies (such as efficient stomatal control over a wide range of resistances, bulbs or underground portions which can persist for a long time, and rapid growth and seed production) will have an advantage. M. trifoliata, for instance, may have lower r_{leaf} values than C. aquatilis, but it has tubers buried in the peat and pond sediments. Like other sedges (and grasses, as well) Carex aquatilis has a network of fine roots, and underground stems which persist for more than one year (Chapin and Chapin 1981).

Previous authors (Bailey and Davies 1981; Lafleur 1988) have noticed a large variability in r_{leaf} over a span of a few hours. It has been suggested that r_{leaf} will change over the growing season (Jones 1983), and through the day as well. Stoner and Miller (1975) and Lafleur (1988) found that r_{leaf} tends to be low in the morning, and increases through the afternoon and evening. There were not enough measurements to derive clear patterns from the Ekwan data.

Although no single climate variable exerts a strong influence on leaf resistance, temperature seems to be slightly more important than solar irradiance, wind, and VPD. The signs of the regressions agree with expectations: r_{leaf} increases with temperature and VPD, and decreases with wind speed and solar intensity. The temperature relationship is particularly interesting. In theory, r_{leaf} will be high for colder temperatures, reach a minimum at moderate ones, and rise again when it becomes extremely warm. The cardinal temperatures at which these changes occur will presumably vary from species to species. The Ekwan data only cover a range between 10 and 30 ^{o}C. For another coastal subarctic sedge species, Rouse, Hardill, and Lafleur (1987) found that r_{leaf} was substantially higher for temperatures below 10^{o}C. Studies indicate that the intensity of solar radiation only becomes important once it falls below a certain threshold brightness, which represents the minimum required for photosynthesis (Simpson 1981, Fig. 35). In this data set, wind is probably only worth considering for its influence on the porometer. This particular design can react adversely to high winds (Lafleur, pers. comm., 1987). In nature, increased wind speed might have some impact on evapotranspiration by decreasing the thickness of the "laminar boundary layer" of still air between the leaf surface and the turbulent atmosphere through which the water vapour must diffuse (Jarvis and McNaughton 1986; Oke 1978, chap. 4). Prolonged wind abrasion and rubbing against other plants could also damage the stomata, making them less airtight.

There is a possibility that winds could have affected the porometry results by forcing outside air into the cup. This could make readings artificially low, by adding moisture to the dry air which is pumped in by the machine. Alternatively, it could raise the values by removing saturated air so it took longer for the humidity to build up. There are other sources of error inherent in the Ekwan Point data. Carbon dioxide concentration and soil temperature were not measured, and there was no reliable way to gauge soil moisture at the meadow site. Also, leaf water potential, which is an important indicator of the plant's internal water status, was not determined. Courtin and Mayo (cited in Stoner and Miller 1975) note that arctic vegetation tends to have low leaf water potentials (i.e. a fairly high degree of internal water stress) even when it is growing in standing water. One of the species exhibiting this property was a northern subspecies of _Carex aquatilis_ . In addition, there is the possibility of time lags affecting stomatal response at a given moment. Dehydration can have long-lasting effect on plants, and even a few days of high VPD's could influence r_{leaf} after weather conditions have changed (Jones 1983).

The PCA analysis brought forth some interesting results which are confirmed by the other forms of analysis, and by theory. The R^2 values for the individual regressions confirm that air temperature, leaf temperature, and VPD are strongly correlated, and that these 3 terms account for more variation in r_{leaf} than solar radiation or wind. PCA can be a useful and powerful tool (terBraak 1983), with the ability to present large amounts of data in "elegant" simplified graphical form. The PCA output seems to imply that there are certain weather conditions which favour low leaf resistance (under 400 s/m, in this case). Cool (20°C or under), moist (VPD of 0.8 kPa or less), sunny (in excess of 500 W/m^2) conditions seem to coincide with low r_{leaf}. Resistances are higher for hot, dry, and/or overcast weather.

Given such a complicated problem as the relationship between r_{leaf} and climate, there are many possibilities for further research. First of all, _Carex aquatilis_ is of particular interest to botanists and ecologists, since it exhibits considerable variation in stomatal placement and frequency within the species (Standley 1986). Unlike its relatives, it is amphistomatous, with stomata on both sides of the leaf. No attempt has been made yet to investigate relationships between stomatal distribution and leaf resistance for _Carex aquatilis_ subspecies, three of which occur in the Hudson Bay Lowlands: _C. aquatilis_ var. _aquatilis_ , var. _stans_ , and var. _altior_ (Dutilly, Lepage, and Duman 1954, Scoggan 1959, Hulten 1964, Hulten and Fries 1986). Unrelated plants growing in the same habitat should also be studied, since there are few measurements available for subarctic wetland vegetation. Recent advances in porometer design should allow a wider range of species to be sampled. In addition, the increasing availability of computer software for use in ecology has made PCA and other intricate forms of statistical analysis more accessible to the general user. These should be explored, to determine whether they are of use in examining plant/climate relationships. Of course, any form of statistical manipulation, even the common and accepted procedures such as calculating averages and linear regressions, must be viewed critically. (See Huff's landmark book How to Lie with Statistics, 1954.) Any attempt to resolve patterns out of a set of numbers risks overlooking or distorting the data. Having a large amount of data is no guarantee of accuracy, either. The multivariate models constructed by Lafleur (1988) accounted for only 50% of the variation in leaf resistance, illustrating how difficult and complex the vegetation-atmosphere relationship is.

Although it would be desirable to be able to predict the canopy resistance of a vegetated surface using only environmental variables, as of now it is not possible to do this with a high degree of accuracy. In addition, the models may only be relevant for the particular region where the data were collected, and may not be applicable for different plant species. A number of studies have been done which attempt to estimate the evaporation over specific types of vegetation (Lafleur and Rouse 1988; McNaughton and Black, and Gay and Stewart, cited in Oke 1978; Bailey and Davies 1981; and others). This has practical applications for the development of water and energy budgets for various regions, but is fraught with difficulties, even for meadows, plantations, and agricultural crops consisting of large areas of relatively homogeneous vegetation. For natural habitats, the situation becomes even more complex, due to the presence of varying concentrations of different species which may exhibit a range of stomatal resistances under similar environmental conditions. Interspecific competition for water and sunlight may be considerable (Jarvis and McNaughton 1986). In addition, the evaporation from bare soil or standing water beneath the vegetation makes it difficult to determine how much of the total evaporation above the surface is due to the plant canopy, especially when the vegetation has a wide variation in density. "Homogeneity" in nature is largely a myth. Most uncultivated vegetation, even a uniformly-green meadow, is a mixture of different species, with ground cover ranging from complete down to minimal or nonexistent. In a plant canopy, the maximum stomatal conductivity of leaves can be affected by leaf position, age, health, and past environmental history (Jarvis and McNaughton 1986). Evidently, the study of evapotranspiration in various environments, particularly natural ones, remains open to investigation. Given the fact that the environmental and physiological influences on vegetation canopies, and their complex interrelationships, are not well understood (Bailey and Davies 1981), it is not surprising that previous investigators have found it difficult to accurately predict how stomatal resistances change under field conditions, even for agricultural crops.

If high leaf resistances are related to high temperatures, high VPD, and low light conditions, as the PCA suggests, then the projections of some recent climate change studies may be of particular relevance. Sophisticated general circulation models incorporate a doubling of atmospheric carbon dioxide, which could happen within a few generations at current emission rates. They forecast an increase of as much as 3 to 5 ^{o}C in mean summer surface temperatures for the James Bay region (Washington and Meehl 1984). In itself, the increase in CO_2 is not expected to have a significant impact on plant growth, on the regional scale (Jarvis and McNaughton 1986), although leaf resistance has been found to increase for high concentrations of this gas (Simpson 1981). However, the expected shift in the surface-atmospheric energy budget due to retention of heat by "greenhouse gases" like carbon dioxide, methane, and water vapour, could have a number of far-reaching effects on northern regions. The growing season might lengthen, and the potential for evaporation could increase during the summer months. If the spring sunlight, which would otherwise be reflected back into space by ice and snow, is instead absorbed by the ground, there would be more energy available for evaporating surface moisture. In permafrost areas such as the Canadian arctic and subarctic, the thickness of the "active layer" (maximum depth of yearly thawing) could increase, affecting water storage and drainage. A significant decrease in soil moisture for the James Bay Lowlands has been predicted, along with a reduction in cloud cover and summer precipitation and an increase in potential evaporation (Manabe and Wetherald 1986). The net result could be a much warmer, drier growing season.

Not only would this produce atmospheric conditions which would, if the Ekwan porometry results are correct, increase stomatal resistance, but it would also reduce the amount of water available through the soil. Even if water stress is not severe enough to completely shut down the stomata, it can reduce photosynthesis (Johnson and Caldwell 1975) and hence, plant growth and productivity (Stoner and Miller 1975). Stressed plants would probably be more susceptible to disease and mechanical damage, and their capacity to reproduce through seed and vegetatively might also be affected (Stoner and Miller 1975). Possibly, plants like *Menyanthes trifoliata* , which are adapted to the wettest areas, would be even worse off than *Carex aquatilis* , since they have less control over water loss (Stoner and Miller 1975).

It seems that widespread drought in the subarctic regions would lessen primary productivity, at least in the short term, with possible implications for key herbivorous species such as geese (*Branta* , *Chen* , and *Anser* spp.) and lemmings (*Lemmus* and *Dicrostonyx* spp.). Over time, the ecosystem would begin to adapt to the changed conditions. The vegetation mixture, and the evaporation characteristics of the canopy, would be altered, as species from warmer, drier habitats gained a competitive advantage and expanded their ranges northwards. *Carex aquatilis* var. *altior* , the taller, southern subspecies, might migrate as far as Hudson Bay. Species themselves might evolve in response to their environment. There could be shifts in water and nutrient absorption capabilities, plant height and growth rate, root:leaf production ratios, and leaf longevity and number. Even within a single species, there is enough genotypic variation to allow for the possibility of adaptation through natural selection (Chapin and Chapin 1981; Chapin and Oechel 1983). Genotypes which are better suited to longer growing seasons and warmer, drier summers might become dominant. Standley (1986) found that stomatal density and distribution on *Carex aquatilis* , for example, are governed more by heredity than by the availability of soil moisture during the period of leaf development. (Jones (1983), though of the opinion that leaf position in the canopy and growing conditions generally can account for significant stomatal variation, also acknowledges a genetic influence.)

Of course, all such reasoning is pure speculation. It is extremely difficult to forecast the long-term environmental impacts of climate change with any degree of accuracy. However, if the computer models have any credibility, and the increasing consensus among climatologists and ecologists is that they do, then the art of prediction will become very important.

Figure 1

Map of Ekwan Point

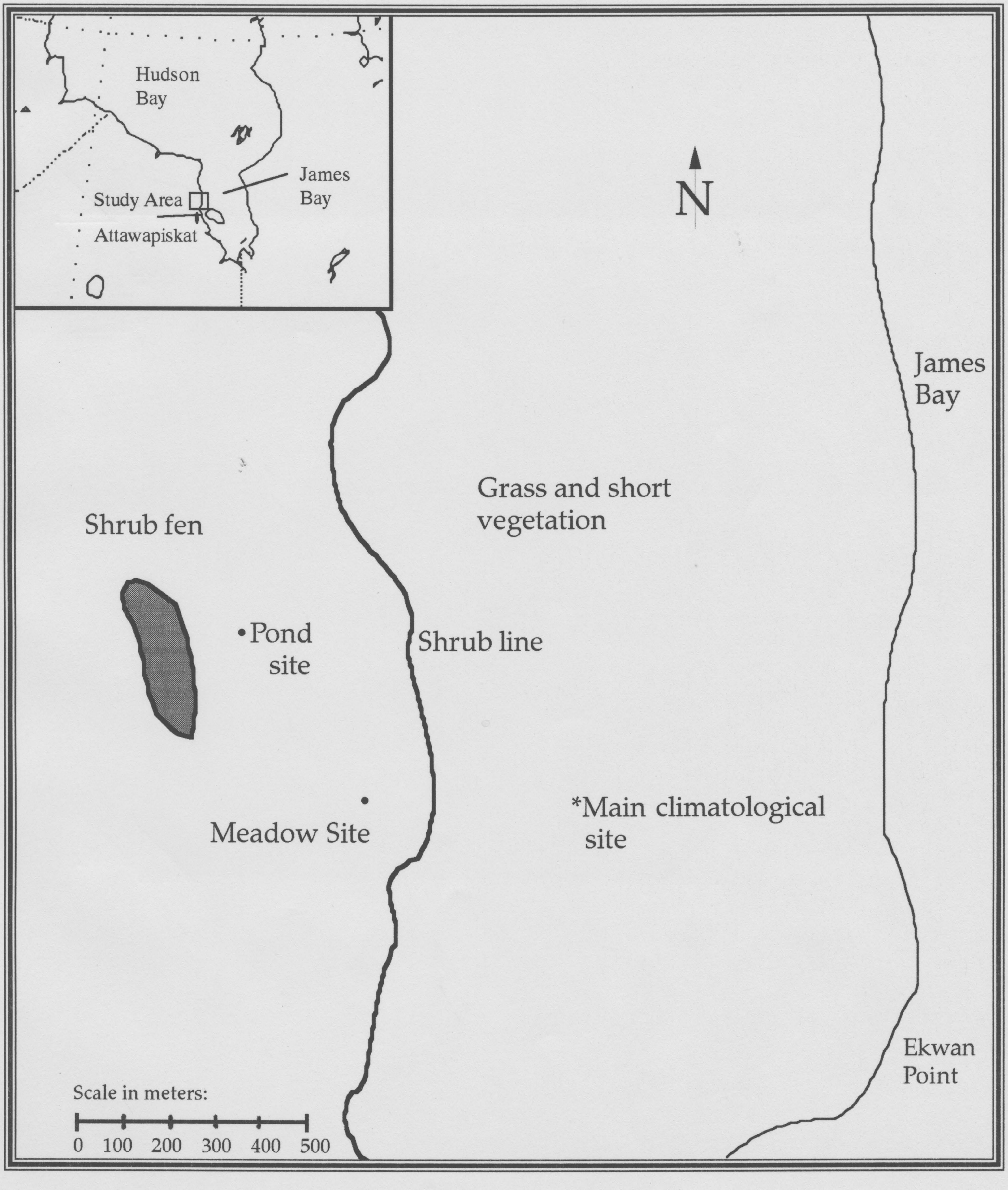


Fig. 2a: Main climatological site, Ekwan Point.

Fig. 2b: Main mast at main climatological site
(wind direction, wet and dry-bulb sensors)

Fig. 2c: Meadow site, looking east towards shore. "Open" plot in foreground.

Fig. 2d: Pond site, looking north. *Carex aquatilis*, with *Menyanthes trifoliata* in foreground. Beach ridge at extreme left.

Fig. 3

Growth Curves for <u>Carex aquatilis</u> at Meadow Site

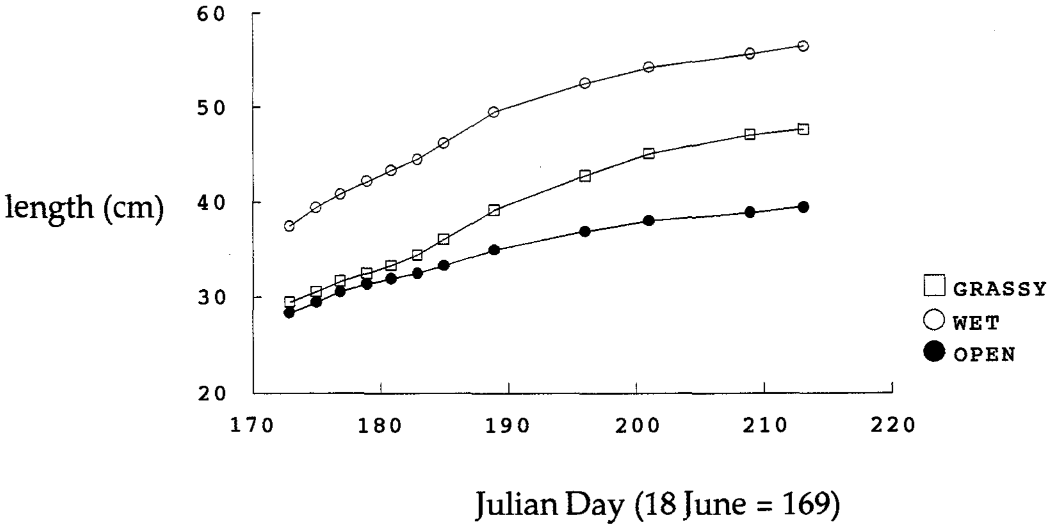


Fig. 4

Time Series of Pond Site Variables

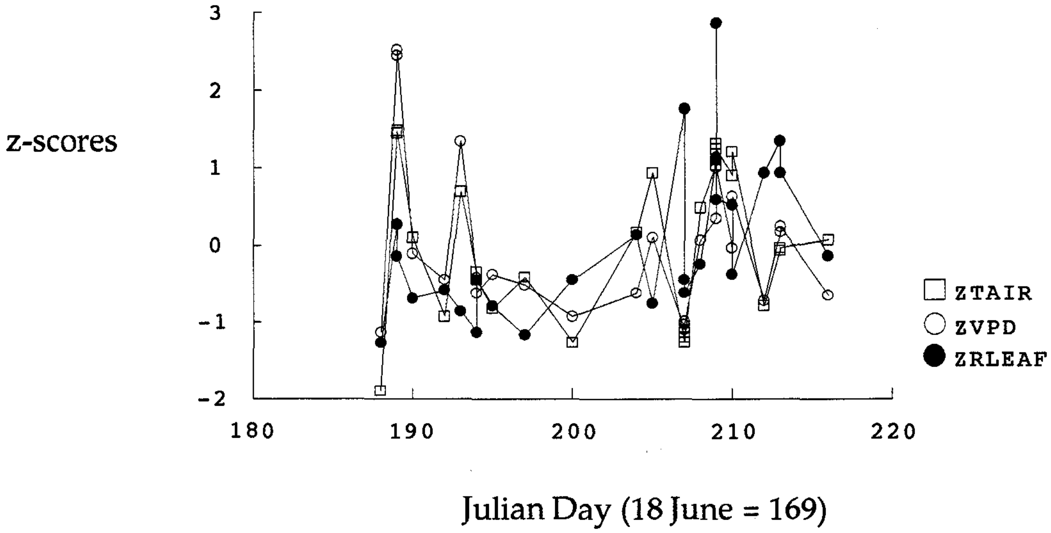
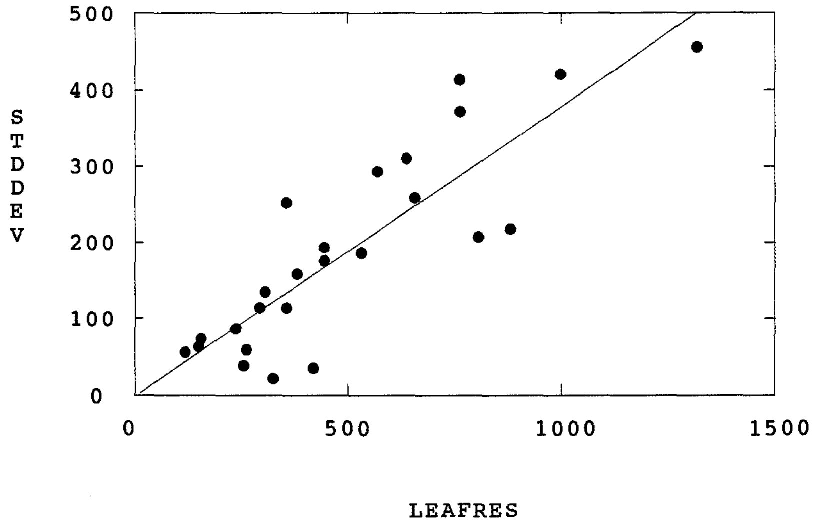


Fig. 5

Relationship Between Leaf Resistance Means and Sample Standard Deviation



STDDEV=-3.715+0.381*LEAFRES

Fig. 6

PCA Scores (no leaf resistance)

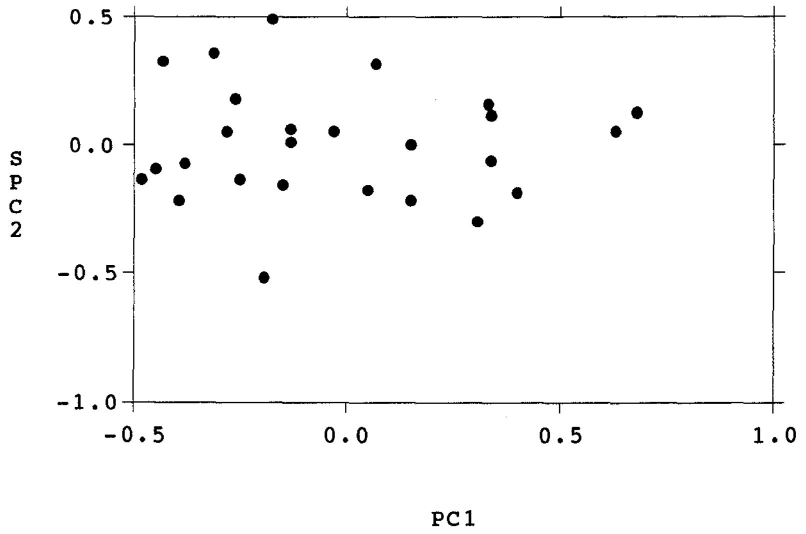


Fig. 7

PCA scores (with leaf resistance)

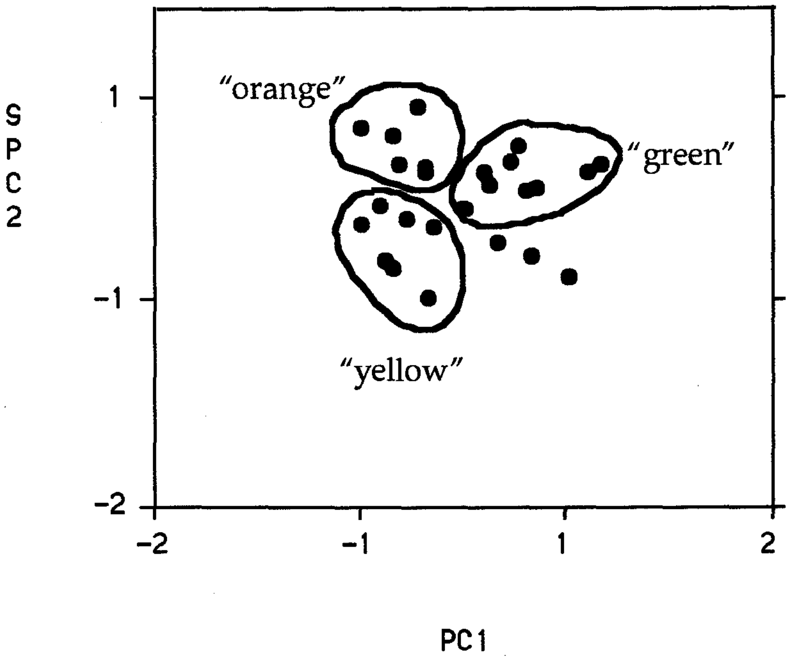


Fig. 8

PCA Components (no leaf resistance)

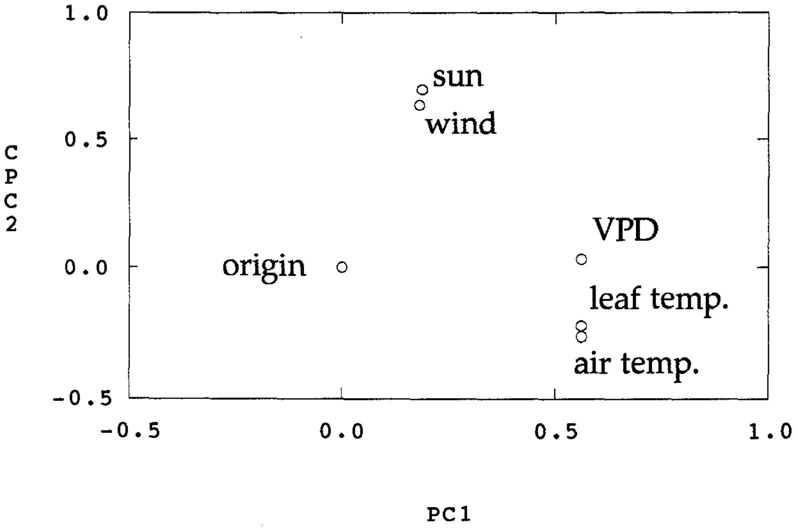


Fig. 9

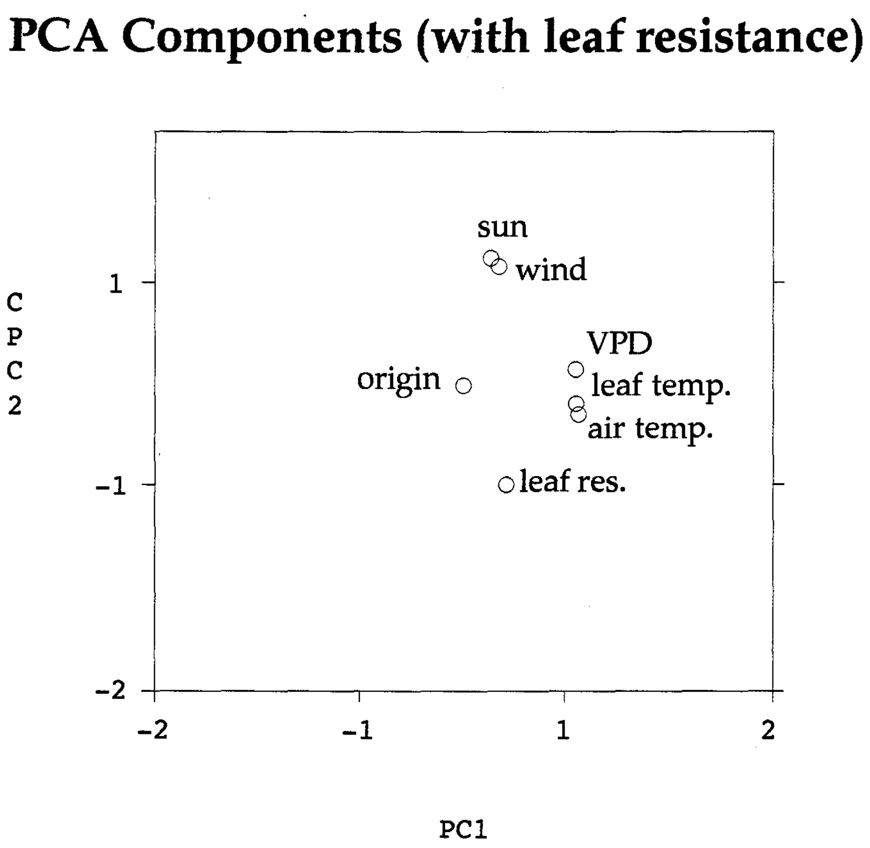

PCA Components (with leaf resistance)

Fig. 10

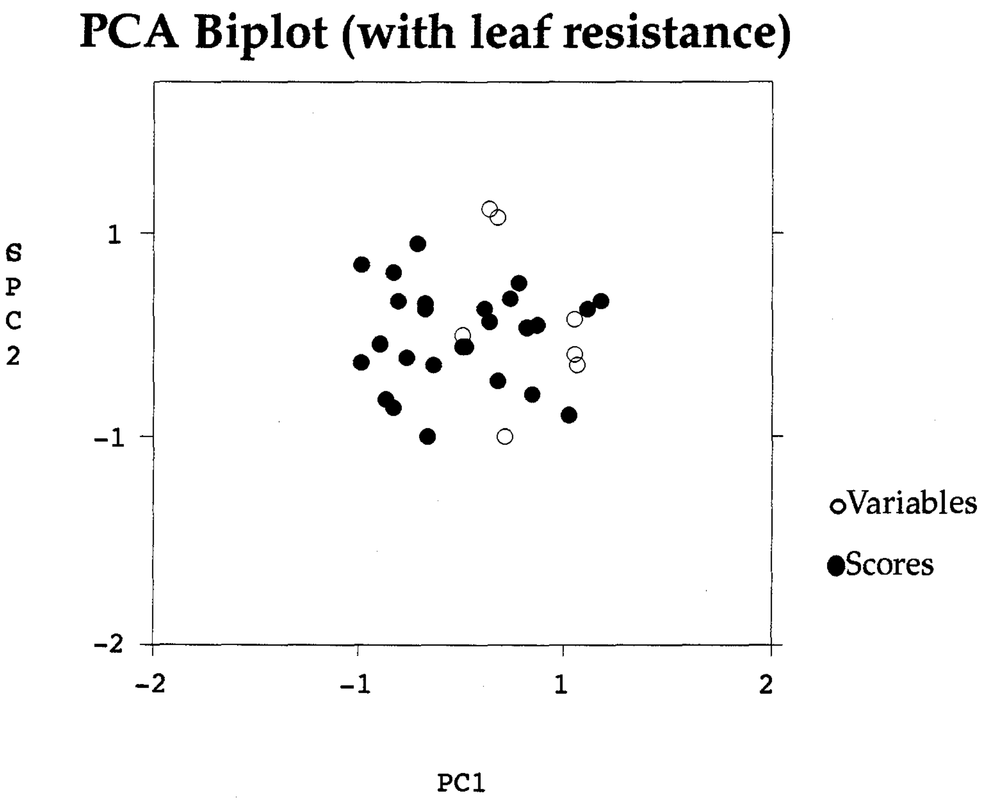

PCA Biplot (with leaf resistance)

Table I:

Estimated changes in aboveground crop production
(*Carex aquatilis* , dry mass in g/m^2)

Julian Day	Avg. (Meadow)	Avg. (Pond)
169	72	n.a.
174	104	n.a.
179	111	n.a.
182	n.a.	456
183	133	n.a.
189	158	n.a.
195	104	601
201	173	606
209	158	n.a.

Table II:

Changes in Leaf Area: Dry Mass fraction
for *Carex aquatilis* (m^2/kg)

Julian Day	Meadow	Pond
176	13.8	n.a.
179	14.4	n.a.
181	n.a.	14.1
182	13.7	
n.a.		
196	13.3	n.a.
199	n.a.	12.2
201	12.1	13.1

Table III:

Estimated changes in averaged Leaf Area Index for *Carex aquatilis*

Julian Day	Avg. (Meadow)	Avg. (Pond)	Range(M)	Range(P)
174-6	1.4	n.a.	0.7-1.9	n.a.
179	1.6	n.a.	0.9-3.8	n.a.
182	n.a.	6.2	n.a.	5.1–7.2
195-6	1.4	n.a.	1.1-1.8	n.a.
201	2.3	7.3	1.0–4.2	5.1-8.8

Table IV:

R^2 values for study variables (pond data)

variables	r_{leaf}	T_{leaf}	T_{air}	VPD	Sun	Wind
r_{leaf}	–	6.5	9.8	5.5	4.2	0.6
T_{leaf}	6.5	–	91.6	64.8	5.5	0.1
T_{air}	9.8	91.6	–	71.6	0.4	1.2
VPD	5.5	64.8	71.6	–	3.5	16.2
Sun	4.2	5.5	0.4	3.5	–	10.7
Wind	0.6	0.1	1.2	16.2	10.7	–

Table V:

Correlation coefficients (r) for study variables (pond data)

variables	r_{leaf}	T_{leaf}	T_{air}	VPD	Sun	Wind
r_{leaf}	---	0.26	0.31	0.24	-0.20	-0.08
T_{leaf}	0.26	---	0.96	0.81	0.23	0.03
T_{air}	0.31	0.96	---	0.85	0.06	0.11
VPD	0.24	0.81	0.85	---	0.19	0.40
Sun	-0.20	0.23	0.06	0.19	---	0.33
Wind	-0.08	0.03	0.11	0.40	0.33	---

Table VIa:

Variability of r_{leaf} and climate variables (JD 207)

	SOLAR TIME		
Variable	**0800**	**1000**	**1820**
Trends			
r_{leaf} (s/m)	998.2	357.3	307.2
T_{leaf} (°C)	15.2	17.1	14.0
T_{air} (°C)	11.1	12.1	11.6
VPD (kPa)	0.210	0.280	0.246
sun (W/m^2)	453	721	181
windsp (m/s)	4.0	3.2	4.8
wind dir	NE	E	E

Table VIb:

Variability of r_{leaf} and climate variables (JD 209)

Variable	SOLAR TIME 1300	1500	1700
Trends			
r_{leaf} (s/m)	809.1	1319.6	655.8
T_{leaf} (°C)	29.5	30.4	28.6
T_{air} (°C)	26.3	28.2	27.7
VPD (kPa)	1.242	1.814	1.714
sun (W/m^2)	791	487	189
windsp (m/s)	5.8	4.9	5.2
wind dir	S	SW	SW

Table VII:

Listings for multivariate model equations
(prediction of r_{leaf} from climate variables)

Data	Constant	T_{leaf}	T_{air}	VPD	Sun	Wind	R^2(%)
All	608.4	-20.64	29.76	38.0	-0.146	-38.07	15.7
3h noon	248.4	20.29	7.72	-37.8	-0.670	8.30	36.4
"Ran 1"	759.3	-57.98	64.85	-98.3	0.113	-47.95	13.1
"Ran 2"	261.4	-19.66	39.19	-29.8	-0.210	5.97	23.0
"Ran 3"	565.3	-24.83	29.14	88.3	-0.214	-18.10	18.1
"Ran 4"	1057.5	-41.15	43.22	97.4	0.107	-118.90	24.8

Table VIII:

r_{leaf} prediction accuracy

Session	real r_{leaf}	fitted	95%CI	95%PI	40% real
"Ran 1"(s/m)					
1891	572.9	263.4	y	y	n
2041	531.6	606.1	y	y	y
2081	421.0	461.9	y	y	y
2092	1319.6	464.7	n	n	n
2093	655.8	55.8	y	y	n
2161	446.9	586.9	y	y	y
"Ran 2"					
1922	324.2	334.5	y	y	y
1941	156.9	453.8	n	y	n
2003	358.2	234.2	y	y	y
2071	998.2	318.3	n	y	n
2073	307.2	426.6	y	y	y
2101	640.8	611.4	y	y	y
"Ran 3"					
1881	119.6	158.5	y	y	y
1901	294.2	356.4	y	y	y
1951	256.8	473.3	y	y	n
2071	998.2	359.2	n	y	n
2091	809.1	434.0	y	y	n
2101	640.8	526.5	y	y	y
"Ran 4"					
1931	242.6	568.9	n	y	n
1942	356.2	540.2	y	y	n
1971	153.0	525.7	n	y	n
2051	267.5	524.8	y	y	n
2072	357.3	605.1	y	y	n
2131	881.3	392.5	n	y	n

Table IXa:

Description of PCA groups

Variable	Summary	"Yellow"	"Green"	"Orange"
r_{leaf} (s/m)	range	307.2-998.2	242.6-881.3	119.6-358.2
	median	446.9	434.1	206.9
	mean	536.9	508.1	228.1
T_{leaf}(°C)	range	14.0-22.5	19.5-32.3	14.5-21.1
	median	17.1	28.0	15.6
	mean	17.5	26.9	16.9
Tair (°C)	range	11.1-20.6	19.1-29.2	7.0-17.3
	median	14.4	24.8	13.6
	mean	15.2	24.3	13.2
VPD(kPa)	range	0.210-0.554	0.935-2.810	0.169-0.718
	median	0.474	1.206	0.648
	mean	0.407	1.560	0.538
Sun(W/m^2)	range	121.2-721.0	558.2-796.0	374.3-852.0
	median	247.7	705.0	703.8
	mean	309.3	690.3	659.2
Wind(m/s)	range	3.03-5.22	3.40-6.78	4.43-7.24
	median	4.56	5.57	5.77
	mean	4.23	5.54	5.87

Table IXb:

Table of relative comparisons for PCA groups

Variable	"Yellow"	"Orange"	"Green"
r_{leaf}	high	low	high
Tleaf	low	low	high
Tair	low	low	high
VPD	low	low	high
Sun	low	high	high
Wind	low	high	high

Table X:

Results of r_{leaf} comparisons: meadow/pond sites

Session	Mean	Median	Range	Std.dev.	95% C.I.
1921	353.6	351.2	318.8-404.3	20.6	M>P
1922	324.2	318.8	306.6-396.1	20.0	
1931	434.5	423.4	237.8-688.5	137.0	M>P
1932	242.6	228.0	128.7-404.7	85.0	
2081	446.5	429.5	235.0-649.2	108.9	M=P
2082	421.0	416.4	369.4-506.0	32.6	

(meas. in s/m)

Table IX:

Results of r_{leaf} comparisons: *C. aquatilis* /*M. trifoliata*

Session	Mean	Median	Range	Std.dev.	95% C.I.
1951	256.8	252.2	202.7-343.1	37.8	C>M
1952	189.5	186.2	169.6-235.7	14.3	
2121	761.1	680.8	323.3-1631.8	369.8	C>M
2122	467.0	438.0	269.4-714.5	107.1	

(meas. in s/m)

Appendix A:

Results from stepwise regressions:
All pond data

STEP	1	2	3	4	5	6
Constant	608.4	529.3	416.4	363.7	220.5	493.3
Leaf temp	-21	-19				
(T-ratio)	-0.37	-0.36				
air temp	29.8	31.8	14.7	14.5	13.9	
(T-ratio)	0.59	0.66	1.68	1.70	1.62	
VPD	-38					
(T-ratio)	0.20					
sun	-0.15	-0.15	-0.26	-0.28		
(T-ratio)	-0.34	-0.36	-1.00	-1.16		
wind	-38	-29	-13			
(T-ratio)	-0.44	-0.40	-0.23			
S	298	291	285	279	281	290
R^2	15.74	15.58	15.06	14.86	9.85	
0.00						
				*		

Pond data within 3 hours of solar noon

STEP	1	2	3	4	5	6
Constant	248.18	301.27	317.14	312.34	17.69	437.18
Leaf temp	20	17	18	25	19	
(T-ratio)	0.30	0.34	0.37	2.35	1.67	
air temp	8	10	7			
(T-ratio)	0.13	0.19	0.16			
VPD	-38	-25				
(T-ratio)	-0.14	-0.12				
sun	-0.67	-0.64	-0.65	-0.69		
(T-ratio)	-1.09	-1.33	-1.40	-1.99		
wind	8					
(T-ratio)	0.08					
S	296	282	270	260	286	303
R^2	36.36	36.32	36.24	36.10 *	16.36	0.00

Random model 1

STEP	1	2	3	4	5	6
Constant	759.3	707.2	838.7	522.1	341.6	443.8
Leaf temp	-58	-48	-47	-35		
(T-ratio)	-0.95	-1.28	-1.29	-1.05		
air temp	64.9	56.4	47.3	35.9	5.7	
(T-ratio)	1.13	1.41	1.41	1.19	0.52	
VPD	-98	-97				
(T-ratio)	-0.43	-0.44				
sun	0.11					
(T-ratio)	0.21					
wind	-48	-37	-32			
(T-ratio)	-0.53	-0.51	-0.83			
S	288	278	271	269	270	265
R^2	13.13	12.85	11.73 *	7.89	1.89	0.00

Random model 2

STEP	1	2	3	4	5	6
Constant	261.4	297.3	319.0	268.7	118.8	501.9
Leaf temp	-20	-22	-20			
(T-ratio)	-0.34	-0.45	-0.45			
air temp	39	40	37	20	18	
(T-ratio)	0.74	0.83	0.93	1.95	1.80	
VPD	-30	-23				
(T-ratio)	-0.14	-0.13				
sun	-0.21	-0.20	-0.21	-0.33		
(T-ratio)	-0.44	-0.47	-0.56	-1.20		
wind	6					
(T-ratio)	0.06					
S	300	290	281	274	277	293
R^2	23.00	22.98	22.89	21.92 *	15.28	0.00

Random model 3

STEP	1	2	3	4	5	6
Constant	565.3	459.8	449.9	532.6	371.0	485.3
Leaf temp	-25	-16				
(T-ratio)	-0.28	-0.23				
air temp	29	22	6			
(T-ratio)	0.33	0.30	0.27			
VPD	88	72	87	128	104	
(T-ratio)	0.43	0.38	0.50	1.56	1.27	
sun	-0.21	-0.27	-0.33	-0.35		
(T-ratio)	-0.40	-0.69	-1.21	-1.56		
wind	-18					
(T-ratio)	-0.17					
S	296	286	277	270	276	280
R^2	18.11	17.95	17.66	17.28	8.22	0.00
				*		

Random model 4

STEP	1	2	3	4	5	6
Constant	1057.5	973.4	765.3	588.5	212.1	528.3
Leaf temp	-41	-31	-28			
(T-ratio)	-0.68	-0.84	-0.79			
air temp	43.2	35.3	40.5	15.7	16.0	
(T-ratio)	0.82	0.98	1.24	1.73	1.74	
VPD	-97	-90				
(T-ratio)	0.43	0.41				
sun	0.11					
(T-ratio)	0.21					
wind	-119	-103	-80	-71		
(T-ratio)	-1.03	-1.21	-1.27	-1.16		
S	299	289	282	279	281	296
R^2	24.79	24.55	23.69	23.72 *	14.47	0.00

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