Å) through the phosphate oxygens, a situation also found in the orthorhombic form of 3′-CMP. The mean planes of the pyrimidine rings of the two molecules are inclined to each other by 13°. The structure is also stabilized by other hydrogen bonds formed through the water molecules.

A study of the torsion angles shows that the bases in both molecules are in the *anti* conformation, which is considered energetically more favorable (*7*). In both molecules the hydroxyl O(5′) orients itself in the *gauche-gauche* configuration. The puckering of the sugar ring is found to be C(2′)-*endo* in both molecules, the C(2′) atoms being displaced by 0.49 Å (molecule A) and 0.56 Å (molecule B) from the mean plane through the remaining four atoms in the respective sugar rings. In standard notation, the envelope (*E*) conformation of the sugar rings may be described as ^{2}E for both molecules (*8*). Earlier nuclear magnetic resonance studies have also strongly favored the C(2′)-*endo* puckering of the molecules in solution. Such a puckering results in the least energy barrier to rotation about the glycosidic bond (*9*). This may also result in the less energetically favored *syn* conformation of the pyrimidine ring becoming permissible under special conditions, such as binding of the molecule to the enzyme (*1*).

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Polar Desert Adaptations of a High Arctic Plant Species

Abstract. *Plants of* Saxifraga oppositifolia *(Saxifragaceae) possess metabolic adaptations that allow them to grow successfully in polar desert microenvironments. Net photosynthesis (net carbon uptake) continues to be positive during drought until the leaf water stress declines to the range of −21 to −29 bars, which is considerably below the nonstress range of 0 to −10 bars. The plants can survive leaf water stresses of at least −44 bars in the field and leaf water stresses of −55 bars in a growth chamber.*

The interacting factors of restricted moisture availability and a short low-temperature growing season make polar desert environments among the most severe for plants (*1*). The lack of a regularly recurring summer moist period has resulted in the exclusion of most vascular plants, including all annuals, from arctic polar desert sites. Only about two dozen species of perennial vascular plants occur in the hundreds of thousands of square kilometers of true arctic polar desert habitats (*2*). These plants complete their annual cycle of growth in an environment characterized by low soil moisture contents, droughts which are unpredictable in both occurrence and duration, and low total precipitation. The severity of drought in polar deserts suggests that those species which do occur should possess adaptations of growth and metabolism similar to those of at least some of the perennial plants found in deserts of more temperate regions.

Saxifraga oppositifolia L., a semiwoody cushion plant, is a long-lived perennial with a circumpolar distribution in the Arctic and in some alpine regions. The species occupies a broad range of habitats, including many polar desert sites (*3*). I studied several populations of this species on polar desert microsites in Truelove Lowland on the north coast of Devon Island (76°N) in the Canadian Arctic Archipelago. Most of the surface of the lowland is mesic to wet tundra meadow, but a series of raised beach ridges in the lowland provides well-drained polar desert microsites. The research sites were on beach ridges located in the middle of the lowland.

The beach ridge surfaces (*4*) are covered by a desert pavement of pebbles overlying several meters of coarse gravel. The plant cover is a sparse polar desert vegetation consisting primarily of low-growing plants of *Salix arctica* and *Saxifraga oppositifolia*, along with scattered individuals of about seven other species of vascular plants. The vascular plant density averages about 45 individuals per square meter, with a total cover of about 17 percent of the ground surface. Lichens cover many of the pebbles of the pavement, with windblown lichen fragments present in depressions. The total lichen cover frequently exceeds 50 percent on the dry beach ridges. Mosses generally have a maximum cover of 1 percent.

At this latitude, the sun remains above the horizon from late April until the third week of August. Flowering and leaf growth of *Saxifraga oppositifolia* on the exposed beach ridges begin by the end of the first week of June. Fruit and leaf development can be temporarily interrupted by drought or snow cover during the growing season, and then continue when conditions become more favorable.

The records of 1969 through 1971 indicate that the total precipitation of the "usual" growing season on this lowland (mostly scattered rain showers) is less than 50 mm. During all 3 years of this study there were periods of several weeks in the growing season with no precipitation. The research sites were free of snow from late June until late August or early September. The zone of thaw had progressed below a depth of 15 cm (below most roots) prior to 10 June. There was a drought in each of the three growing seasons. The most severe drought occurred during 1971, when no precipitation fell from the time of snowmelt until early July. During this drought, the soil water availability remained below −15 bars for about 4 weeks (Fig. 1). The drought coincided with relatively high levels of solar radiation resulting in leaf water stresses (ψ_{leaf}) of between −25 and −35 bars in plants of *Saxifraga oppositifolia* during midday (*5*). The maximum leaf water stress on a clear day was −44 bars; the plants survived this stress. The atmospheric vapor pressure deficits during this period ranged between 0.3 and 4.0 mm-Hg. In 1969 and 1971, the period of drought occurred early in the growing season. In 1970, however, the drought lasted from late July until mid-

August. Under stable weather conditions, the daily leaf water stress usually was greatest in early afternoon, with minimum stress values occurring near midnight or shortly thereafter. Under such conditions, the daily range in leaf water potential values was about 6 bars.

Foehn winds from the nearby Devon ice cap, lasting from a few hours to several days, can occur at any time (*3*). The driest atmospheric conditions measured during this study occurred during a foehn wind in late July 1969. The wind lasted continuously for 46 hours; during this time the relative humidity remained between 46 and 60 percent, while air temperatures ranged between 11° and 17°C at plant height. The sky was partly cloudy to clear during the wind. Prior to the start of the foehn, the midday leaf water stress of *Saxifraga oppositifolia* was −6 bars. At the end of the foehn, the leaf water stress has increased to −17 bars. Reproductive and vegetative growth of these plants occurs in the field while leaf water stress ranges between −10 to −20 bars.

Six plants of *Saxifraga oppositifolia* were transplanted from a Devon Island beach ridge to a growth chamber in the Phytotron at Duke University in which it was possible to simulate polar desert conditions (*6*). These plants were grown under leaf water stresses less severe than −10 bars (nonstress conditions) for 6 months. The chamber was then programmed for simulated severe foehn conditions (*7*), and no further water was added to the pots. After 7 days of this stress, the plants were just beginning to show leaf wilting at leaf water potentials of −55 bars. At this point watering was resumed; all of the plants survived and resumed growth.

The field observations suggest that the net photosynthesis (net carbon uptake) remains positive at leaf water stresses of at least −15 bars. A second set of plants was transplanted to a growth chamber and grown under the nonstress conditions described above for 6 months. After 6 months, water was no longer added to the pots and the net photosynthesis was monitored daily with an infrared gas analysis system (*8*) until it declined to zero. At this time, the leaf water stresses of the plants ranged from −21 to −29 bars (mean of three replicates, −25 bars). These data confirm field observations of these plants under drought conditions. Leaf water stresses greater than this range were measured only occasionally in the field during the most severe drought periods.

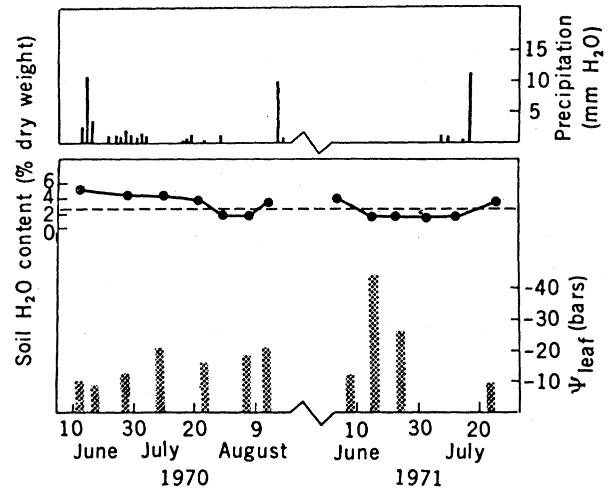

Fig. 1. Field measurements of precipitation, soil water content, and leaf water stress (Ψ_{leaf}) for two growing seasons on a polar desert microsite. The dashed line indicates a pressure level of −15 bars for soil water retention.

Although the environment and vegetation of arctic polar desert regions have been described, there are no quantitative data on the ranges of metabolic adaptations of polar desert vascular plants (*9*). On the basis of the data presented in this report, *Saxifraga oppositifolia* can be thought of as a species with several adaptations to desert conditions, namely, photosynthetic ability and water metabolism. Other arctic plants outside of polar desert habitats generally grow in mesic to hydric environments, lacking severe drought stress, regardless of local precipitation regimes. The generally well-drained, deeper thawing soils of polar desert sites contribute significantly to the severe summer droughts. The Barrow region of Alaska, for example, has low annual precipitation, but the Barrow tundra is poorly drained and does not develop severe soil water deficits. Dennis (*10*) has reported that water stresses measured in many plants in the Barrow region are usually in the range of −1 to −5 bars; the most severe stresses he measured were about −10 bars. Thus, from the point of view of plant-water relations, the Barrow tundra is not a desert-like environment except perhaps in some microsites.

On the other hand, the Devon beach ridge plants possess the ability to continue to grow during more severe water stress (−10 to −20 bars) and the ability to tolerate and survive severe water stress (−44 to −55 bars). Such abilities are similar to those reported for woody perennials of the deserts of the American Southwest (*11*). These characteristics of drought tolerance, coupled with the recurrent appearance of environmental water stress during growth, indicate that the beach ridge populations of *Saxifraga oppositifolia* are, indeed, polar desert plants.

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4. The data in this report pertain only to dry beach ridge sites having a distinct polar desert microenvironment.
5. All field and laboratory measurements of water potential were made by the dye method with an accuracy of ± 2 bars [E. B. Knipling, *Ecology* **48**, 1038 (1967)]. All data are the means of three replicates.
6. Growth chamber conditions were as follows: a continuous light intensity of 0.3 langley min^{-1}; an air temperature of 17°C for 12 hours followed by an air temperature of 3°C for 12 hours. Plants were grown in a mixture of vermiculite and washed gravel; nutrients were added by use of half-strength Hoagland's solution.
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