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3.4 Water Potential of Antarctic Soils

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Summary: Matric effects contribute less to the water potential of soils in the McMurdo Dry Valleys of Antarctica)informally known as the Ross Desert) than do the mineral salts of these soils. Since soil samples from the same area can exhibit 10-fold differences in mineral content, it is important that water potentials be determined on the same samples used for microbiological unvestigations. The psychrophilic yeast content of fertile soil samples from the arid highlands of the McMurdo Dry valleys indicated that the effective water content of these soils did not exceed ca. 4.5% (v/w).

Zusammenfassung: Das Wasserpotential von Böden in den McMurdo Dry Valleys (auch Ross Desert genannt) wird weniger von matrikalen Effekten bestimmt als vom chemischen Potential der Mineralsalze. Da Bodenproben desselben Gebietes Unterschiede im Mineralgehalt bis zum zehnfachen aufweisen können, ist es wichtig, daß Wasserpotentiale an derselben Probe bestimmt werden, an der auch mikrobiologische Untersuchungen vorgenommen werden. Der Gehalt an psychrophilen Hefen in fertilen Bodenproben der trockenen Hochlagen in den McMurdo Dry Valleys ist ein Indikator dafür, daß der effektive Wassergehalt dieser Böden ca. 0.45% (Volumen/Gewicht) nicht überschreitet.

1. INTRODUCTION

The ahumic/frigic (see CAMPBELL & CLARIDGE 1987) soils of continental Antarctica have been reported to have a high mineral salt content. The major ions in aqueous extracts of McMurdo Dry Valley (Ross Desert) soils were Na^+, Ca^{2+}, Mg^{2+}, K^+, Cl^-, and SO_4^{2-} in varying ratios (BOCKHEIM 1979, CAMPBELL & CLARIDGE 1978, CLARIDGE & CAMPBELL 1977). Investigators whose concerns were primarily pedologic have pointed out that the waning of marine influence with distance inland and altitude was indicated by decreasing ratios of Cl^- to SO_4^{2-} and Na^+ to Ca^{2+} as the results of rock weathering became relatively more important (KEYS & WILLIAMS 1981, CAMPBELL & CLARIDGE 1977). Other investigators (CAMERON 1971, 1972, 1974; VISHNIAC & HEMPFLING 1979) have examined the chemistry of McMurdo Dry Valley soils as microbial habitats, but without evident recognition of the importance of scale, that is, that microorganisms occupy microhabitats. Since logistic problems limit the amount of soil which can be transported under deep freeze for subsequent examination of biota, sample storage has varied with intended use (CAMERON 1974, VISHNIAC & HEMPFLING 1979). When samples are being collected for differing purposes with differing transport requirements, it is reasonable to assume that, although collected contiguously, the samples may reflect any heteogeneity in the soil. VISHNIAC & HEMPFLING (1979) analyzed samples which had the same site designations as the samples used for isolating microbiota, but which were in fact collected separately (presumeably contiguously) and transported by ship in an unfrozen condition. The results of biotic investigations of these and additional collections called our attention to the possible importance of local heterogeneity.

The only known indigenous biota of arid upland soils in the McMurdo Dry Valleys are psychrophilic yeasts (VISHNIAC & HEMPFLING 1979). Although these yeasts can reliably be preserved by lyophilization (as is typical of yeasts, fungal spores, and bacteria), and may therefore be presumed to tolerate freeze-drying in nature, they unexpectedly failed to exhibit marked xerotolerance during growth (VISHNIAC & HEMPFLING 1979). When some soil samples failed to yield isolates of psychrophilic yeasts, low water potential appeared to be a possible explanation. We therefore used the remaining portions of the samples collected beginning with the austral summer of 1980—1981 to examine factors affecting water potential. In addition to confirming the hypothesis that inhibition by high mineral salt content limits the distribution of psychrophilic yeasts in McMurdo Dry Valley soils (VISHNIAC & KLINGLER 1988), the results indicated that the heterogeneity of these soils dictates that chemical analyses be performed on the same, relatively small, well-mixed, samples used for biotic surveys and have allowed calculation of the biologically effective water content of Dry Valley soils.

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2. MATERIAL AND METHODS

Soil samples were collected during the austral summers of 1980—81 through 1983—84 by the junior author and other members of Dr. E. I. Friedmann's Antarctic Cryptoendolithic Microbial Ecosystems group.

Samples were collected aseptically in sterile "Whirl-Pak" bags, kept frozen during transport, and stored at –20 to –80° C. Samples massed from ca. 50 to ca. 500 g, depending upon the size of the soil pocket at a particular site and depth. All subsamples were taken after mixing the bag contents aseptically, while the bag rested on a bed of dry ice in a laminar flow hood. The methods used for yeast isolation varied with soil microbial content and over time, as improvements were devised (see VISHNIAC 1983, 1985). The final method, for unproductive samples still in sufficient supply, was simulated in situ enrichment by the addition of up to 0.5 ml diluted liquid medium M3C (VISHNIAC 1985) to 5 g aliquots of soil (in sterile test tubes) held at 10° C. Selected soil samples were examined for major cation content and water potential. When sufficient quantities of soil were available, the samples were analyzed in triplicate. Standard deviations are provided in the appropriate tables.

The exchangeable cation contents (Ca^{2+}, K^{+}, Mg^{2+}, and Na^{+}) were extracted with an excess of ammonium acetate and analyzed by atomic absorption spectrometry according to the methods of THOMAS (1982) and BAKER & SUHR (1982), using a Perkin-Elmer model 373 absorption spectrometer. Total cationic microequivalents were summed as microatoms per gram times charge.

Water potential was determined by adding glass-distilled water in amounts ranging from 0.025 to 25% (v/w) to 10 g of air-dry soil in a 7 ml polythene scintillation vial and allowing the contents of the vials to equilibrate before inserting a Wescor HR33-T dewpoint microvoltmeter (model 5103). The vials were then sealed and placed in a 25° C water bath. Measurements were taken 24 and 48 hrs later. Simulated soils were prepared by mixing washed (in 4 N HCl and glass-distilled water) sand, kaolinite, and montmorillonite (Ward's Natural Science Corp., Rochester, NY) in the indicated proportions. The particle size of the sand ranged from 250 to 850 µm (bulk density 1.72 ± 0.02, saturated at 17% water); clay particle size was in both cases ≤ 150 µm. Particle size was determined by sieving (USDA standard testing sieves of numbers 20, 60, 100 and 200 mesh). Sand containing 3% montmorillonite had a bulk density of ca. 1.74 and was saturated at 25% water; sand containing 10% montmorillonite a bulk density of ca. 1.81 and was saturated at 38% water. Sand containing 10% kaolinite had a bulk density of ca. 1.76 and was saturated at 18% water.

The effect of major cations on the growth rate of a model indigenous yeast, *Cryptococcus vishniacii* var. *asocialis* isolate A801-30bY33, was determined in GPY medium (glucose, 1.0% w/v; peptone, 0.5% w/v; yeast extract 0.3% w/v) containing either no additional cations or added Na^{+} (as NaCl) or Ca^{2+} (as $CaCl_2.2H_2O$). Neutral $CaCl_2.2H_2O$ solutions were prepared by dissolving $CaCO_3$ with the equivalent of dilute HCl. A flask to which mannitol was added served as control for the osmotic neutrality of these cations. Mannitol is not assimilated by this yeast and was therefore presumed to be a neutral osmoticum. Osmosity (the molar concentration of an equi-osmolar NaCl solution in g-mol/liter) was calculated from WEAST (1978). The media were inoculated with exponentially growing cells to an optical density (OD) at 650 nm of ca. 0.2. Precultures and experimental cultures were incubated at 10° C in a shaking water bath (New Brunswick Scientiefic Co., model G-76). Growth was followed by determining OD_{650nm} with a Bausch and Lomb Spectronic 70 spectrophotometer. These experiments were intended only to determine the interchangeability, with regard to growth inhibition, of the dominant cations in Antarctic soils. The results have only indirect bearing on in situ growth and are not comparable to the halotolerance data presented in VISHNIAC & KLINGLER (1988). The complex medium necessarily used to keep the calcium in solution is far richer in organic compounds than Antarctic soil and its ingredients contained unknown quantities of cations.

3. RESULTS

The major cation content of 31 soil samples is shown in Table 1. As expected, calcium and/or sodium ions predominated in almost every soil. Since most of the samples were taken at relatively high altitudes and within an area more restricted than that sampled by pedologists, it is not surprising that no consistent correlation between altitude or distance inland and the Na^{+} to Ca^{2+} ratio can be seen. However, a rather large variation in ratio was

Sample	Cation (µA g−1±S.D.*): Ca2+	K+	Mg2+	Na+	Total cationic µEquivalents
Wright valley, Asgard Range: Mt. Odin 1520 m alt.					
A801–28a**	35.62	2.47	7.24	17.35	105.54
:Linnaeus Terrace (below Mt. Oliver) 1600 m alt.					
A801–b	0.93	1.01	7.10	19.86	36.93
A812–1a	0.61	1.57	13.78	30.54	60.89
A823–1	1.35±0.24	0.66±0.005	1.86±0.16	2.62±0.77	9.70
A823–2	0.77	0.75	3.44	10.16	19.33
A823–4	10.52	1.49	7.30	9.66	46.79
A834–57	4.29	1.84	15.63	18.75	60.43
A834–59	1.25	0.62	1.27	1.47	7.13
:Mt. Oliver ca. 1800 m alt.					
A801–25	5.24	2.53	16.45	33.54	79.45
:Valley W of Mt. Oliver 1430 m alt.					
A801–29a	1.89	0.35	2.65	2.46	11.89
–29b	2.53	0.51	3.13	2.36	14.19
: Tyrol Valley (hanging valley, Mt. Baldr) 1530 m alt.					
A801–30a	2.05	0.93	3.24	6.68	18.37
–30 b	5.89	1.04	3.96	6.16	26.90
Wright Valley: slope above Don Juan Pond, ca. 500 m alt.					
A823–5b	12.70±3.13	0.53±0.03	0.83±0.06	72.81±3.51	100.40
–5c	20.28±1.67	0.58±0.08	0.90±0.07	63.81±3.51	106.75
Wright Valley: Dais ca. 900 m alt.					
A812–22a	31.30	3.58	6.27	40.33	119.05
A812–23a	1.35	0.42	0.94	1.07	9.85
–23b	3.80	0.69	1.65	2.06	13.65
A834–53	5.57	0.96	2.26	2.16	18.78
Wright Valley, Olympus Range: Mt. Dido ca. 1600 m alt.					
A823–3	2.06±0.20	0.74±0.09	3.04±0.28	8.53±1.64	19.47
A834–51b	1.09	0.43	1.51	1.37	7.00
Taylor Valley: lower Taylor Valley ca. 100 m alt.					
A823–10	17.39	24.55	5.55	96.09	166.52
: Nussbaum Riegel ca. 400 m alt.					
A834–65a	8.42	1.49	1.04	2.96	23.37
–65b	10.20	1.56	1.19	4.16	28.50
Beacon Mts.: University Valley (hanging valley with small glacier) ca. 1900 m alt.					
A812–20a	2.69	0.57	2.08	1.37	11.48
–20b	1.41	0.42	1.13	1.07	6.57
A834–63a	6.36	1.08	5.75	11.65	36.95
A834–66	12.92	3.68	7.10	9.30	53.02
: Arena Valley ca. 1500 m alt.					
A812–24a	2.21	1.07	1.49	2.06	10.53
–24b	2.69	2.05	1.23	4.36	14.25

Tab. 1: Major cation content of McMurdo Dry Valley soils. * Standard deviations are given only for soil samples sufficiently copious for analysis of triplicate subsamples. ** Samples were numbered to indicate the austral summer season (p.e. A801 = the austral summer of 1980-1981) and the site number (p.e. –28) followed by an indication of depth at which the sample was taken. The letter „a" or no letter indicates samples taken between 0–0.5 cm and 1–2 cm; „b", between 1–2 cm and 2–3 cm; „c", between 3 and 5 cm.

observed in the Linnaeus Terrace samples in Table 1, in which Na^{+}: Ca^{2+} averaged 14.12 ± 17.56.

Linnaeus Terrace is a substantially level, south-facing, area of ca. one square kilometer, below Mt. Oliver and above the floor of the Wright Valley. As in most of the dry valley region, its lithologies are varied, with soil derived mainly from weathering of sandstone and dolerite. The heterogeneity of Linnaeus Terrace soils was such that sample A812-1, collected as nearly as possible at a site from which a highly fertile (exhausted, therefore not analyzed) sample had been taken the previous season, turned out to be so salt-laden as to preclude the isolation of psychrophilic yeasts. The variation in ionic content and total cationic microequivalents which can be expected in soil samples collected in the same area is indicated by the Linnaeus Terrace samples, in which Na^{+} (usually the most abundant cation) varied from 1.47 to 30.54 microatoms g^{-1} averaging 13.29 ± 10.38 microatoms g^{-1}, and total cationic microequivalents varied from 7.13 to 60.89 averaging 34.46 ± 22.80 microequivalents g^{-1}.

The water potentials of simulated soils and of selected soil samples as water content was increased are shown in Table 2 and Table 3. The resulting water potential curves are shown in Figure 1. The water potentials given for simulated soils are assumed to be due solely to matric forces. While matric forces can be seen to affect water potential, osmotic forces clearly played the major role in determining water potential in McMurdo Dry Valley soils. Dry Valley soils differ in this respect from developed soils containing humus and greater proportions of silt and clay, in which matric forces typically play a major role in determining water potential. Figure 1 indicates that the samples A801-25, A812-1a, and A823-5b have essentially the same water potential, –3.2 MPa, at a water

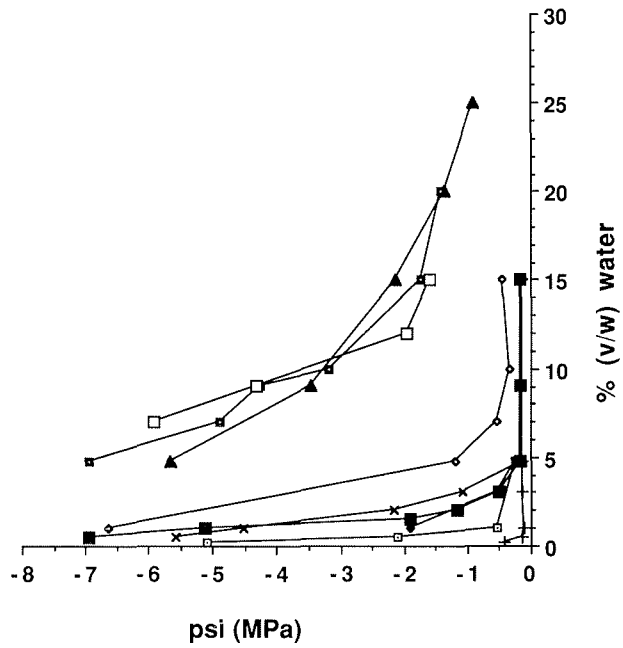

Fig. 1: Water potentials with increasing water content of simulated soils and Antarctic soil samples: +, sand; -, sand + 3% montmorillonite; ✻, sand + 10% kaolinite: ▲, A823-5b; ■, A812-1; ❑, A801-25; ◊, A823-4; ◆, A834-63a; ❑, A834-65b.

	Soil: sand	3% kaolinite	10% kaolinite	3% montmorillonite
% water (v/w)				
0.25	–0.42±0.13			
0.50	–0.13±0.09	–4.69±0.35	–5.57±0.43	–6.93±0.46
1.00	–0.10±0.10	–1.63±0.13	–4.53±0.27	–5.13±0.18
1.50				–1.90±0.27
2.00		–0.12±0.03	–2.17±0.20	–1.17±0.44
3.00	–0.13±0.10	–0.10±0.03	–1.08±0.35	–0.51±0.17
4.76	–0.13±0.13	–0.13±0.03	–0.15±0.03	–0.16±0.05
9.10	–0.13±0.13	–0.14±0.08	–0.15±0.03	–0.16±0.03
15.00	–0.13±0.07			–0.17±0.03

Tab. 2: Water potentials (MPa ± S.D.) of simulated soils.

	Soil: A801–25	A812–1	A823–4	A823–5b	A834–63a	A834–65b
% water (v/w)						
0.25						–5.10±0.60
0.50						–2.10±0.13
1.00			–6.63±0.44		–1.90	–0.54±0.10
3.00			–1.64		–0.53	
4.76		–6.93	–1.20	–5.67±0.13	–0.26	–0.26±0.13
7.00	–5.93	–4.90±0.30	–0.53			
9.10	–4.33±0.13	–4.27		–3.47±0.27		–0.07±0.05
10.00		–3.20	–0.33			
12.00	–1.97					
15.00	–1.60	–1.73	–0.47	–2.13		
20.00		–1.43		–1.37±0.17		
25.00				–0.90±0.07		

Tab. 3: Water potentials (MPa ± S. D.) of Dry valley soil samples.

content of 10% (v/w). Yet A823-5b was salt-encrusted sand, the matric potential of which should not have exceeded that of washed sand (Tab. 2), while A801-25 was a sample consisting of wind-packed yellow silt and clay with between 3/4 and 4/5 of the osmotic potential of A823-5b. The silt and clay content of sample A801-25 was unusual; samples typically consisted of sandy gravel or gravelly sand, as described by CAMPBELL & CLARIDGE (1978). The only sample showing any aggregation of particulates (as well as relatively high clay content) was A834-66, taken near the top of the slope at the mouth of University Valley.

The effect of Na^+ and Ca^{2+} osmosity on the growth rate of *Cryptococcus vishniacii* var. *asocialis* in liquid culture is shown in Figure 2. Since the specific growth rate (k) is affected more by Na^+ (as chloride) than by Ca^{2+} (as chloride) of equal osmosity, one may question whether 'total cationic microequivalents' is an appropriate reporting category. The addition of $CaCl_2.2H_2O$ of an osmosity of 0.70 to this complex medium appears to have about the same effect on k as the addition of NaCl to an osmosity of 0.525 (i. e., about .5 M NaCl). While physiological adaptation to Na^+ and Ca^{2+} was observed in cultures (at the lower osmosities) which were grown through more than 3 generations, the ratio of effect on k was maintained. Neither cation can be assumed to act only as a neutral osmoticum. Mannitol, at an osmosity of 0.45, did not result in a growth rate significantly lower than the k = 0.104 ± 0.003 generations per hour at 10° C recorded in unamended medium. The *Cr. vishniacii* cells exposed to 13% mannitol were as incapable of utilizing mannitol as sole substrate at the end of this experiment as at its beginning. The effects of these cations were nevertheless sufficiently similar to make total microequivalents the unit of choice in examining the correlation of fertility with mineral salt content.

The correlation of soil mineral salt content with yeast isolation (the indicator of fertility) is shown in Table 4. An earlier comparison of some soil samples in terms of microatoms g^{-1} can be found in VISHNIAC & KLINGLER (1988). Yeasts were isolated from all sites at which the soil contained < 19.47 cationic microequivalents g^{-1}. Fertility was roughly halved in soil samples containing ca. 20 cationic microequivalents; yeasts were not isolated from soils containing > 60.5 microequivalents of the measured cations.

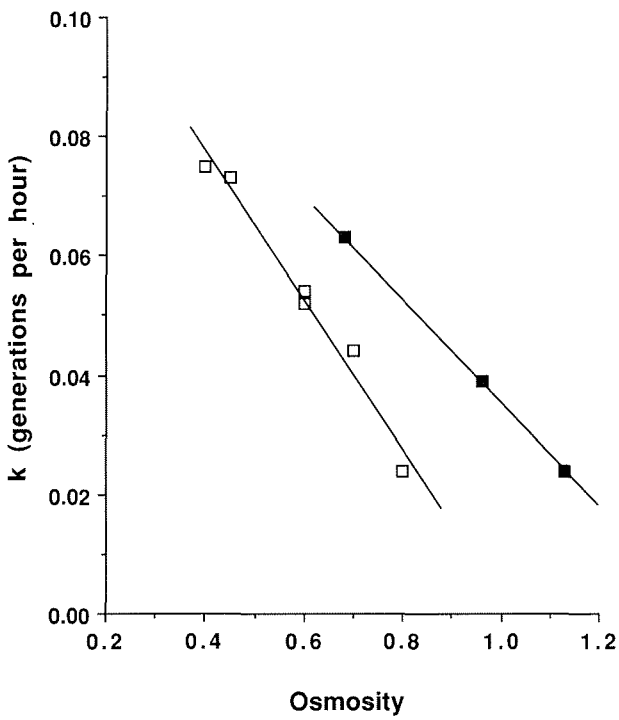

Fig. 2: Change in growth rate of *Cryptococcus vishniacii* var. *asocialis* (grown in a shaking water bath at 10° C) with osmosity of salts added to a peptone-yeast extract-glucose medium: ❑ NaCl, ■ $CaCl_2.2H_2O$. Regression lines drawn by Cricket Graph™ v 1.1 (Cricket Software, 3508 Market St., Philadelphia PA 19104): NaCl, y = 0.1279 — 0.1255x, r = 0.99; $CaCl_2.2H_2O$, y = 0.1219 — 0.0866x, r = 1.00. The rates shown are those of the first 2—3 generations of exponential growth during exposure to these salts. [On subculture into the same media, NaCl of osmosity 0.45 → k = 0.109 (generations 2.45 through 8.95), osmosity 0.60 → k = 0.063 to 0.090 (generations 3.11 through 5.57), osmosity 0.70 → k = 0.053 (generations 2.54 through 4.61); $CaCl_2O$ of osmosity 0.68 → k = 0.104, osmosity 0.96 → k = 0.032 (generations 2.71 through 3.87).]

4. DISCUSSION

Since salt content is the major factor determining water potential in these predominantly sandy soils, the heterogeneity of our samples is likely to have resulted from variation in leaching. These soils are xerous. Water has been called the major factor limiting microbial growth in the McMurdo Dry Valleys (HOROWITZ et al. 1972). CAMPBELL & CLARIDGE (1987, p. 272) have pointed out that while dispersion of mineral salts (rather than accumulation in a salt horizon) is usual in soils with this moisture regime, meltwater may leach soil around

< 19.40 µEquiv. g^{-1}		19.40–60.50 µEquiv. g^{-1}		>60.50 µEquiv. g^{-1}	
A812–20b	6.57	A823–3*	19.47	A812–1*	60.89
A834–59	7.13	A801–30b	26.90	A801–25*	79.45
A823–1	9.70	A834–65b*	28.50	A823–5a*	100.40
A812–23a	9.85	A801–8b	36.93	A801–28*	105.54
A812–24a	10.53	A834–63a*	36.95	A823–5b*	106.75
A812–20a*	11.48	A823–4*	46.79	A812–22a*	119.05
A801–29a*	11.89	A834–66	53.02	A823–10*	166.52
A812–23b	13.65	A834–57	60.43		
A801–29b	14.19				
A812–24b	14.25				
A801–30a	18.37				
A834–53	18.78				
A823–2	19.33				
% fertile samples	85%		44%		0%
% fertile sites	100%		50%		0%

Tab. 4: Correlation of total cationic equivalents per gram with isolation of psychrophilic yeasts. * Samples from which psychrophilic yeasts were not isolated.

irregularly shaped boulders, though insolation and evaporation can concentrate salts under flat rocks. The occurrence of liquid water depends not only upon the relatively rare and sporadic snowfalls, but on the deposition of snow in sites sufficiently protected that ablation and sublimation do not precede insolation temperatures exceeding the melting point. It has been "observed that the amount of snow reaching the (Linnaeus) terrace varies considerably from year to year and that large snow deposits in the lee of large rocks and in topographic depressions may persist for longer than an annual cycle... to... 2 years later... a snow mound erected in open 1.5 m high, 2 m square base was 1 m high after 1 yr, 0.5 m high after 2 yr" (MCKAY et al. 1984). Leaching is therefore likely to be localized. The salt content of the microhabitat cannot be assumed from the averages of any particular area.

The inverse correlation between yeast isolation and total cationic microequivalents present shown in Table 4 can be used in calculating the availability of water in these soils (Although cation content does not explain the infertility of samples A801-29a or A812-20a). A model Antarctic psychrophile, *Cryptococcus vishniacii* var. *asocialis* (isolate A801-30bY33), grown under simulated in situ conditions in the presence of NaCl, began to be limited in growth rate at a water potential of –1.74 MPa, a figure not significantly different from the –1.8 MPa at which microbial activity peaks in other arid soils (see SKUJINS 1984). The growth rate fell to half maximal, and colonization of sand grains failed entirely below a water content of 5%, at –3.56 MPa (VISHNIAC & KLINGLER in press). The application of these data to water potential curves is illustrated in Figure 3. We have calculated that the most salt-laden fertile sample would have had to contain 4.5% water to raise the water potential to –3.56 MPa (VISHNIAC & KLINGLER in press). In terms of yeast growth and distribution, the highest biologically functional water content attained by these soils therefore appears to be ca. 4.5%, shown as the upper boundary of fertile areas of water potential in Figure 3. The site of A834-57 apparently did at some point contain at least 4.5% water, though the fertility of this sample was low (of the order of 0.2 biotypes g^{-1}). Simulated in situ enrichment was required for the isolation of a single yeast biotype. The site of A823-4, like those of half the samples in the second column of Table 4, apparently did not chance to receive sufficient water. We have calculated that the soil samples listed in the first column of Table 4 would reach water potentials allowing growth and dispersal in the presence of the least amount of water, between 1 and 2.5%, which permitted growth in simulated in situ experiments (VISHNIAC & KLINGLER in press). The figure of 4.5% for maximum water content of soils in the McMurdo Dry Valley highlands is obviously imprecise, given the assumptions which were made in its calculation. It serves to introduce a concept, biological effectiveness, which allows comparisons to be made between habitats in which the actual variations in water potential and biological activity cannot, in practise, be directly measured over significant time periods.

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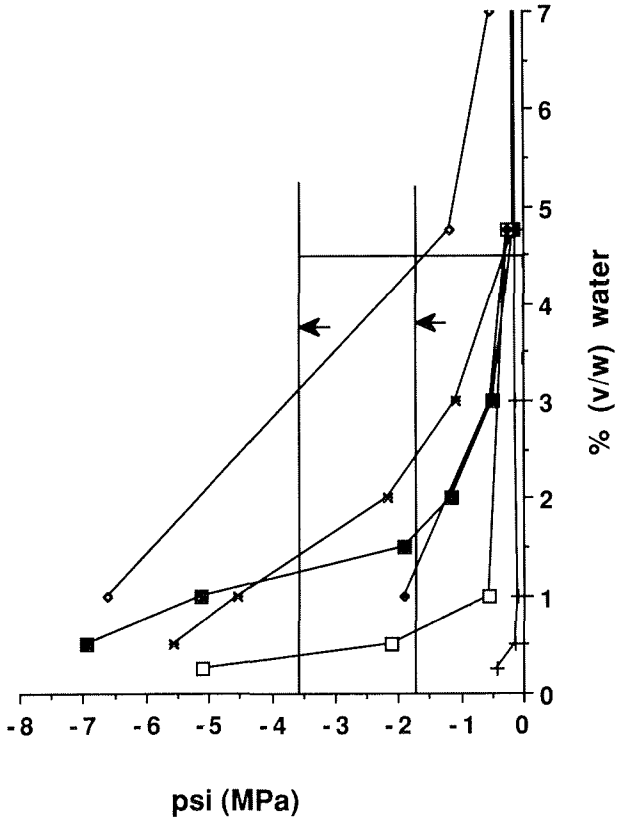

Fig. 3: Areas of soil water potential allowing growth of indigenous psychrophilic yeasts. The box on the right indicates the area in which water potential does not limit yeast growth, with an arrow indicating the lower limit. The adjacent (left) box indicates an area of water potentials limiting yeast growth, with an arrow indicating the point at which further colonization is inhibited. For comparison, the potential curves of sand (+), sand + 3% montmorillonite (-), and sand + 10% kaolinite (✻) are included. ⊿ = A834-65b, ◆ = A834-63a, ◊ = A823-4.

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