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The Diversity of Volume Regulatory Mechanisms

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Abstract

Mammalian cells utilize a wide variety of cell volume regulatory mechanisms. For rapid adjustment of cell volume cells release or accumulate ions through respective channels and transport systems across the cell membrane. The most widely used mechanisms of cell volume regulatory ion release include ion channels and KCl symport. Ion uptake is most frequently mediated by Na^+ channels, Na^+, K^+, $2Cl^-$ cotransport, and Na^+/H^+ exchange. Chronic adjustment of cell osmolarity is accomplished by the formation or accumulation of organic osmolytes, molecules specifically designed to create intracellular osmolarity without interfering with cellular function. The most widely occurring osmolytes are sorbitol, inositol, glycerophosphorylcholine, betaine, taurine, and amino acids. The osmolytes are either synthesized by or transported into shrunken cells. During cell swelling osmolytes can be rapidly degraded or released. Any given cell may utilize several volume-regulatory mechanisms. Moreover, different mechanisms are utilized in different tissues. The diversity of cell volume regulatory mechanisms allows the cells to defend the constancy of cell volume against a myriad of challenges with relatively little impairment of cellular function.

Key Words
Osmolytes
Ion channels
Na^+/H^+ exchanger
Na^+, K^+, 2Cl cotransport
KCl symport
Intracellular Ca^{2+}
Stretch-activated channels

Introduction

In order to survive cells must be able to maintain their volume within certain limits. Cell volume depends on water flux across the cell membrane, which is generally highly permeable to water. Water flux is driven by osmotic gradients. The low mechanical resistance of animal cell membranes precludes an increase in the hydrostatic pressure gradient. Thus, any osmotic imbalance across the cell membrane will lead to respective alterations

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of cell volume. A multitude of factors challenge the constancy of cell volume. These include alterations of extracellular osmolarity, nutrient uptake, activation of ion channels and transport systems at the cell membrane, formation or cleavage of proteins or glycogen from or to osmotically more active monomers, and the degradation of organic substances to CO_2 and H_2O.

A challenge to cell volume can only be accomodated if osmotic equilibrium across the cell membrane is maintained by the cell volume regulatory mechanisms. These mechanisms include ion transport across the cell membrane on the one hand, and formation or disposal of organic osmolytes on the other.

Several mechanisms for cell volume regulation are usually employed in parallel. Moreover, different cell types utilize different cell volume regulatory mechanisms. As a result the number of ion transport mechanisms and organic osmolytes employed is large.

The present review is a synopsis of the diverse cell volume regulatory mechanisms utilized in different cell types. The review concentrates on mammalian cells and does not consider comparative aspects of cell volume regulation. Moreover, the reader is encouraged to consult earlier reviews on various aspects of cell volume regulation [1–45], osmolytes [4, 46–48], and the role of cell volume in regulation of cell function [49–56].

Volume-Regulatory Ion Transport

Volume-regulatory ion transport is the most rapid means of decreasing or increasing intracellular osmolarity. The transport systems are most conveniently disclosed by step changes of extracellular osmolarity.

If extracellular osmolarity is abruptly decreased, the cells swell due to osmotically driven water influx (across the cell membrane). Cell swelling then triggers volume regulatory extrusion of ions and osmotically obliged water, leading to regulatory cell volume decrease (RVD).

If extracellular osmolarity is abruptly increased, the cells shrink due to osmotically driven water efflux. Cell shrinkage then triggers volume regulatory uptake of ions and osmotically obliged water, leading to regulatory cell volume increase (RVI).

Regulatory Cell Volume Decrease (RVD)

Volume-regulatory ion release is accomplished by both ion channels and ion transport systems (table 1). Cells can utilize more than one of the listed transport systems and thus be able to regulate their volume even if one of the volume regulatory transport systems is inhibited.

Most cells release ions, at least in part, by activation of ion channels. Cell swelling can lead to the activation of K^+ channels, of anion channels or of both. While the K^+ channels are selective, the anion channels have been found to be permeable to chloride, bicarbonate, and organic osmolytes [57–62].

The activation of K^+ channels is only effective for volume regulatory ion release if the anion channels are operating in parallel, since otherwise the cell simply hyperpolarizes to the K^+ equilibrium potential without significant net loss of ions. Volume regulation by activation of anion channels requires the operations of K^+ channels, since otherwise the cell depolarizes towards the equilibrium potential for anions.

Volume-regulatory K^+ channels include the Kv1.3 (n-type K^+ channel) [63], the Kv1.5 channel [64], and the minK channel [65, 66].

Volume-regulatory anion channels include the ClC-2 channel [67–71] and BRI-VDAC [72]. I_{Cln} is either a volume regulatory anion channel [73–78] or a regulator thereof [79]. The putative role of P-glycoprotein (or MDR

Table 1. Ionic mechanisms of cell volume regulation (figures are reference numbers)

Regulatory cell volume decrease

Parallel or separate activation of K^+ and/or Cl^- channels

Lamprey erythrocytes 323
Mouse erythrocytes 324
Human erythrocytes 325
Frog erythrocytes 326
Platelets 327
Lymphocytes 5, 75, 119, 157, 328–342
Thymocytes 329
HL-60 leukemic cells 343, 344
Neutrophils 345, 346
THP-1 and HL-60 myelocytic cells 347
HeLa cells 348–351
Ehrlich ascites tumor cells 15, 16, 352–361
Fibroblasts 362, 363
Proximal renal tubule 142, 159, 364–373, 375–378
Thin ascending limb of Henle's Loop 379
Medullary thick ascending limb cells 106, 380
Renal collecting duct 374, 381–389
Opossum kidney (OK) cells 390
Madin Darby canine kidney (MDCK) cells 45, 57, 61, 391–399
Airway epithelial cells 400–408
Esophageal cells 409, 410
Intestinal epithelial cells 411–425
Colonic epithelial cells 412, 426
Colonic tumor cell lines 94, 95, 97, 427–433
Secretagogue stimulated HSY 434
Salivary duct cells 435
Hepatocytes 312, 319, 436–448
Biliary epithelium 449
Skate hepatocyte 450
Vas deferens epithelial cells 451
Retinal pigment epithelium 452–456
Eye lens 457
Nonpigmented retinal epithelium 458
Ciliary ocular epithelial cells 459–462
Vestibular dark cells 463
Corneal epithelial cells 464
Lacrimal glands 465
Sweat glands 466
Rat epididymal cells 58, 467
Turtle colon 468
Necturus choroid plexus 469
Necturus gall bladder 470, 471
Necturus enterocytes 416, 472
Frog proximal tubule 473–476
Frog skin 152, 477–481
A6 cells 482–488
Amphibian urinary bladder 489–493
Thyroid follicle cells 494
Endothelial cells 495–499
Endocardial endothelial cells 500
Ciliary body epithelial cells 501
Vascular smooth muscle cells 108
Cardiac myocytes 502–506
Myoblasts 507
Skeletal muscle 508
Pancreatic β cells 509–511
Chromaffin cells 512–513
Astrocytes 514–523
Glioma cells 59, 524
Neurons 525–531
Neuroblastoma cells 532
Cochlear hair cells 533
Osteoblasts 534–536
Osteoclasts 537
Osteosarcoma cells 538
Xenopus oocytes 539

Activation of K^+/Cl^- symport

Erythrocytes from
- Toadfish 540–542
- Trout 543
- Birds 22, 544–545
- Sheep 107, 546–556
- Horse 557
- Pigs 558
- Dogs 559–562
- Rabbits 563, 564
- Rat 565
- Man 566–576

Ehrlich ascites tumor cells 109, 577
Trout hepatocytes 578
Necturus gall bladder 579
Choroid plexus 104, 469
Pigmented retinal epithelium 456
Thymocytes 580, 581
Vascular smooth muscle cells 108, 582

Parallel activation of K^+/H^+ exchange and Cl^-/HCO_3^- exchange

Amphiuma erythrocytes 111, 583–587
Corneal epithelium 110
Frog skin 588

Release of HCO_3^-

Mammalian proximal renal tubule 45, 370, 589–591
Necturus proximal renal tubule 592

➤

Table 1 (continued)

Regulatory cell volume decrease (continued)

OK cells 105, 593
MDCK cells 57, 594
Osteosarcoma cells 595

Inhibition of K^+/H^+ ATPase
Gastric epithelium 596

Activation of Na^+/Ca^{2+} exchange and Ca^{2+} ATPase
Dog erythrocytes 112, 562, 597, 598
Mollusc erythrocytes 599, 600
Elasmobranch erythrocytes 601

Activation of unselective cation channels
Inner medullary collecting duct 602
Toad urinary bladder 493
A6 cells 603
Atrial cells 604
(see also Table 2)

Inhibition of Na^+ conductance
Ehrlich ascites tumor cells 353

Inhibition of Na^+/K^+ ATPase
Cardiac myocytes 605

Stimulation of Na^+/K^+ ATPase
Synpatosomes 606, 607
Helix neurons 608

Stimulation of Na^+ ATPase
Various tissues from squid, shrimp and teleost fish 113
Neurons 609

Decrease of gap junction conductance
Pancreatic acinar cells 610

Regulatory cell volume increase

Parallel activation of Na^+/H^+ exchange and Cl^-/HCO_3^- exchange
Erythrocytes from
- Amphiuma 111, 540, 541, 583–585, 611–613
- Rat 565
- Pig 614
- Dog 112, 155, 561, 615
- Man 616

Lymphocytes 119, 132, 334, 617–624
Ehrlich ascites tumor cells 625
Medullary thick ascending limb 626, 627
Medullary collecting duct cells 161, 163
Renal inner medulla cells 135
Isolated proximal tubule 628
OK cells 629
MDCK cells 630, 631
Rabbit urinary bladder 632
Intestine 633–635
Salivary glands 636
Gill chloride cells 637
Necturus gallbladder 638–641, 643
Bladder carcinoma cells 642
Cornea epithelium 644
Retinal pigment epithelium 454
Fibroblasts 645
Renal mesangial cells 153
Vascular smooth muscle cells 646, 647
Cardiac cells 648
Barnacle muscle 153
Glial cells 649
Neurons 650, 651
Osteosarcoma cells 652
Osteoclasts 653
Chinese hamster ovary cells 132
Xenopus oocytes 654

Activation of Na^+, K^+, $2Cl^-$ (or NaCl) cotransport
Erythrocytes from
- Birds 22, 544, 545, 655–660
- Rats 565, 661, 662
- Ferret 663, 664
- Man 665, 666
- Rabbit 667

Myocytes 668, 669
Human fibroblasts 670
L cells 671
SV-transfected 3T3 cells 672
HeLa cells 351
Ehrlich ascites tumor cells 16, 118, 145–148, 673–679
Proximal tubule 628, 680
Medullary thick ascending limb 6, 198, 681–684
Medullary collecting duct 163
Salivary glands 151
Parotis 685
Pancreas 686
Intestinal cells 417, 687
Tracheal epithelial cell 688, 689
Frog skin 152, 479, 480
Shark rectal gland 149, 690
Gill chloride cells 637
Retinal pigment epithelium 455, 456, 691
Trabecular meshwork cells 692
Alveolar epithelial cells 693

Table 1 (continued)

Pigmented ciliary or retinal epithelium 456, 694	*Inhibition of Na^+/K^+ ATPase*
Vestibular dark cells 695	Erythrocytes 662
Endothelial cells 499, 696, 697	*Activation of Na^+ or cation channels*
Astrocytes 698, 699	Cortical collecting duct 116
Glioma cells 700–702	Airway epithelia 115
Squid giant axon 143	Hepatocytes 117
Cardiac cells from chick 703	Mast cells 114
Vascular smooth muscle cells 647	*Inhibition of K^+ and/or Cl^- channels*
Skeletal muslce cells 704	Proximal tubule 712, 713
Osteoblasts 705	Thick ascending limb 714
Osteosarcoma cells 652	MDCK cells 630
Pancreatic β-cells 139	Airway epithelia 715, 716
Xenopus oocytes 706	Vas deferens epithelial cells 451
Activation of Na^+/K^+ ATPase	Hepatocytes 9, 717
Renal cortical cells 707	Frog skin 477, 718
Thick ascending limb 162, 681	Urinary bladder 492, 719
Cortical collecting duct 708	Gallbladder 720
Hepatocytes 709	Intestine 419
Intestine 419	Corneal epithelial cells 464
Retinal pigment epithelium 710	Heart cells 669, 703
Lens epithelium 710	Neurons 721, 722
MDCK cells 711	
Cardiac myocytes 605	
Hepatocytes 9	

protein) in cell volume regulation has been a matter of debate [80]. It has been proposed to be a volume-regulatory anion channel [81–86], an ion channel regulator [87–90], or possibly unrelated to cell volume regulation [18, 91–101]. The anion exchanger AE 1 of fish erythrocytes, but not of mammalian erythrocytes, confers an anion channel permeable not only to Cl^- but also to the organic osmolyte taurine [102, 193]. Regardless of the mechanism of action, additional channels must be operative in regulatory cell volume decrease.

Some ion channels are activated by cell membrane stretch which is believed to occur during cell swelling (table 2). Most of the stretch-activated channels (SACs) are rather unselective cation channels. At the negative potential difference across the cell membrane net Na^+ entry is expected to exceed net K^+ release through unselective cation channels and the channels are thus not expected to directly serve cell volume regulation. On the other hand, Ca^{2+} entering through those channels may activate Ca^{2+}-sensitive K^+ channels and thus allow volume-regulatory K^+ release [104–106]. In fact, swelling increases intracellular Ca^{2+} in many cells, an effect frequently required for efficient regulatory cell volume decrease (table 3). Ca^{2+} may enter the cell through Ca^{2+}-permeable ion channels or be released from intracellular stores. In other cells, however, Ca^{2+} does not increase and/or Ca^{2+} is not required for regulatory cell volume decrease.

Besides ion channels, the most frequently utilized transport system for volume-regulatory ion release is electroneutral KCl cotransport [25, 107–109].

Table 2. Mechanosensitive ion channels (figures are reference numbers)

Stretch-activated unselective cation channels	
Ehrlich ascites tumor cells	352, 723, 724
Frog renal proximal tubule cells	474, 475, 725
Necturus renal proximal tubule cells	726, 727
Frog diluting segment	728
Choroid plexus	104
Teleost urinary bladder	729
OK cells	593
Rat liver cells	730
Corneal epithelium	731
Fetal lung	732
Retinal glial cells	733
Neuroblastoma cells	734
Endothelial cells	735, 736
Heart	604
Vascular smooth muscle cells	737, 738
Mesangial cells	739
Osteoblasts	740
Osteosarcoma cells	741
Human fibroblasts	742
Chick embryonic cells	743
Chick heart	744, 745
Xenopus embryonic muscle	746
Frog oocytes	747–750
Crayfish stretch receptor organ	751
Stretch-activated Ca^{2+} channels	
Vascular smooth muscle cells	752
Mesangial cells	753
Stomach smooth muscle cells	754
Stretch-activated K^+ channels	
Xenopus proximal renal tubule	755
Necturus proximal renal tubules	371, 372, 473, 727
Medullary thick ascending limb cells	106
Intercalated cells of renal cortical collecting duct	756
Colonic cells	757
Astrocytes	758
Molluscan heart cells	759
Pulmonary vascular smooth muscle cell	760
Stretch-activated anion channels	
Renal intercalated cortical collecting duct cell (RCCT-28A) line	386, 761
Stretch-inactivated cation channels	
Supraoptic neurons	762
Neurons	763
Dystrophic muscle	764

Table 3. Intracellular Ca^{2+} activity increases following cell swelling (figures are reference numbers)

Lymphocytes	765–767
Lymphoma cells	766
Proximal tubule cells	768–774
OK cells	105, 593, 775
Medullary thick ascending limb	106, 380
Inner medullary collecting duct	776–778
MDCK cells	779–781
Toad urinary bladder	782, 783
Necturus gallbladder	784
A6 cells	785
Intestinal cells	414, 786–789
HT29 cells	790, 791
Gastric parietal cells	792
Mammary cells	793
Sweat glands	466
Rat salivary cells	794, 795
Choroid plexus	104
Epididymal cells	796
Hepatocytes	797
Vascular smooth muscle cells	798
Astrocytes	520, 799, 800
Neurons	801
Cochlear outer hair cells	802
Chromaffin cells	513
Prolactin-secreting pituitary cells	803–805
Fibroblasts	806, 807
Osteosarcoma cells	652, 808
Intracellular Ca^{2+} activity does not increase following cell swelling	
Lymphocytes	809, 810
Ehrlich ascites tumor cells	677, 811, 812
Retinal pigment epithelium	453
Collecting duct cells	813
Ca^{2+} is required for (normal) regulatory cell volume decrease	
Fish erythrocytes	814
Amphiuma erythrocytes	584, 585
Noetia erythrocytes	815–817
Molluscan erythrocytes	818, 819
Lymphocytes	331, 332, 340, 341
Proximal renal tubule	768, 770, 771, 775, 820
Frog proximal tubule cells	475
Teleost proximal renal tubules	821, 822
Thin ascending limbs of Henle's Loop	379
Medullary thick ascending limb cells	380
Principal cells of collecting duct	823
Inner medullary collecting duct	778, 824

Table 3 (continued)

MDCK cells 779–781, 825, 826	Salivary gland acinar cells 795
Frog urinary bladder 489, 490	Lacrimal glands 465
A6 cells 487	Retinal pigment epithelium 453
Necturus gallbladder 827	Neurons 525, 841
Intestinal cells 412, 414, 428, 786, 787, 789, 828	Astrocytes 519, 522
Nonpigmented ciliary epithelium 458	Neuroblastoma cells 734
Secretagogue stimulated HSY salivary duct cells 434	Chromaffin cells 513
Sweat glands 466	Cardiac cells 504
HeLa cells 350	Osteosarcoma cells 652
Astrocytes 520, 829, 830	**Regulatory cell volume decrease is inhibited by calmodulin antagonists**
Neurons 651	Amphium erythrocytes 585
Barnacle muscle cells 831, 832	Molluscan erythrocytes 601, 815–817, 819
Chick cardiac myocytes 744	Lymphocytes 119, 331–332
Osteosarcoma cells 808	Ehrlich ascites tumor cells 357, 358, 842
(Increase of) Ca^{2+} is not required for regulatory cell volume decrease	Proximal renal tubules 843
Erythrocytes from	Enterocytes 412, 844, 845
Man 325	Necturus gallbladder 827
Frog 326	Nonpigmented ciliary epithelium 458
Lymphocytes 331, 334, 335, 339, 833	Goldfish retinal axon 846
Leukocytes 157	Astrocytes 799, 829, 830
THP-1 and HL-60 myelocytic cells 347	Neurons (brain) 847
Platelets 834	Pheochromocytoma cells 848
Ehrlich ascites tumor cells 352, 357, 812, 835, 836	**Phospholipase C is stimulated by cell swelling or required for regulatory cell volume decrease**
Proximal renal tubule 768, 769	Proximal tubule cells 774
Fish proximal tubule 837	Liver 797, 840
OK cells 593, 723, 775	Ehrlich ascites tumor cells 849
Inner medullary collecting duct cells 380	Astrocytes 850
MDCK cells 397	Skate erythrocytes 851
Intestinal cells 415	
Hepatocytes 444, 730, 838–840	
Rat epididymal cells 467	

In some cells volume-regulatory KCl release is accomplished by K^+/H^+ exchange and Cl^-/HCO_3^- exchange [110, 111] operating in parallel. H^+ and HCO_3^- entering the cell in exchange for KCl form intracellular CO_2, which easily exits the cell by diffusion.

In Na^+-rich erythrocytes cell swelling triggers volume regulatory Na^+ exit through reversal of Na^+/Ca^{2+} exchange and subsequent extrusion of Ca^{2+} through the Ca^{2+} ATPase [112]. In other cells Na^+ is eliminated by a Na^+ ATPase [113].

Regulatory Cell Volume Increase (RVI)

Electrolyte uptake during regulatory cell volume increase is accomplished by activation of Na^+ channels and/or unselective cation channels [114–117], of Na^+, K^+, $2Cl^-$ cotransport [118] and/or of the Na^+/H^+ exchanger [119]. The latter alkalinizes the cell and thus activates the Cl^-/HCO_3^- exchanger. The H^+ and HCO_3^- exchanger and Cl^-/HCO_3^- exchanger are formed from CO_2 within the cell, which is readily replenished by diffusion from the extracellular space. During cell shrinkage cellular electrolyte loss is decreased by inhibition of K^+ and Cl^- channels (table 1).

The molecular identiy of volume regulatory Na^+ and other cation channels is unknown. However, several members of the volume regulatory Na^+, K^+, $2Cl^-$ cotransporters [120] have been cloned [121–125]. Little is known about the volume regulatory role of the cloned Na,Cl cotransporter [126].

Among the cloned Na^+/H^+ exchangers [127–130] NHE-1 [131–133], NHE-2 [131, 134] and NHE-4 [135] are stimulated by cell shrinkage and thus serve regulatory cell volume increase. NHE-3, however, is inhibited by cell shrinkage [131, 134, 136, 137]. Among the cloned anion exchangers, AE 2, but not AE 1, appears to serve RVI [138]. At least, fish AE 1 appears to participate in osmolyte release during RVD (see below).

Certain cells are unable to volume regulate in hypertonic extracellular fluid [16, 18, 139–142], presumably due to increased intracellular Cl^- activity. Osmotic cell shrinkage decreases cellular water thus leading to an increased intracellular Cl^- activity which inhibits volume-regulatory Na^+, K^+, $2Cl^-$ cotransport [18, 125, 143–152] and Na^+/H^+ exchange [151, 153–156]. Lowering of intracellular Cl^- activity may establish the ability to RVI. A decrease of intracellular Cl^- can be accomplished by prior RVD [18, 139, 142, 157–160], by activation of Cl^- channels with cAMP [140] or vasopressin [161–163], or by exposure to short-chain fatty acids which swell the cells by accumulation of the acids together with Na^+, thus triggering volume regulatory Cl^- release [164]. The decrease of intracellular Cl^- activity following any of these pretreatments allows the cell to activate Na^+, K^+, $2Cl^-$ cotransport and/or $Na^+/H+$ exchange and thus to accomplish RVI.

Osmolytes

High concentrations of electrolytes interfere with the structure and function of proteins [165–174]. Moreover, ion transport across the cell membrane modifies the membrane potential and electrolyte homeostasis within the cell. Thus, regulation of cell volume by ion transport across the cell membrane cannot be accomplished without affecting ion sensitive functions of the cell. In order to allow adjustment of cellular osmolarity without accumulation of ions, cells produce osmolytes.

General Properties of Osmolytes

Osmolytes are molecules specifically designed to create osmolarity with little impact on other cell functions [175–188]. In contrast to ions, organic osmolytes are compatible with normal macromolecular function, even at high concentrations [189].

The osmolytes utilized by mammalian cells include polyalcohols such as sorbitol and inositol, methylamines such as glycerophosphorylcholine and betaine, amino acids such as glycine, glutamine, glutamate, aspartate, and taurine [47, 174, 178, 179, 182–184, 190–193], and amino acid derivatives.

The highest concentrations of osmolytes are found in renal medulla, where extracellular osmolarity may be more than fourfold that of isotonicity [178, 187, 188, 194–213]. Moreover, osmolytes are most important for regulation of cell volume in the brain where the rigid skull does not allow expansion of the tissue and neuronal function is not compatible with marked alterations of extracellular ion composition [214–227].

Osmolytes stabilize macromolecules and thus counteract the destabilizing effects of inorganic ions such as K^+, Na^+ and Cl^- [166, 228–234]. Betaine, glycerophosphorylcholine, and inositol counteract the destabilizing effect of urea on proteins [180, 235–242]. A balance between destabilizing (i.e. ions, urea) and stabilizing (i.e. counteracting osmolytes) forces is required for normal cell function [173, 243–249]. To maintain this balance, an increase of urea concentration stimulates a parallel increase of glycerophosphorylcholine [207, 239, 250].

Cellular osmolyte accumulation can be achieved by stimulated uptake, enhanced formation or decreased degradation. Decrease of intracellular osmolyte concentration is accomplished by degradation or release. Generation of osmolytes is a slow process, requiring hours to days [251].

Metabolism of Specific Osmolytes

Glycerophosphorylcholine (GPC) is synthesized by deacylation of phosphatidylcholine under the catalytic action of a phospholipase A_2 which differs from the arachidonyl selective enzyme [205]. GPC is degraded to glycerol-phosphate and choline by GPC phosphodiesterase [47, 179, 252]. The phosphodiesterase is inhibited by hyperosmolarity due to either NaCl or urea which thus leads to accumulation of GPC.

Sorbitol is produced from glucose under the catalytic action of aldose reductase [253–267]. Expression of the enzyme is enhanced by increased ionic strength, but not by hypertonic urea or glyerol [255, 268–273]. A change in osmolarity does not affect mRNA stability or enzyme degradation [271, 274]. The half life of the enzyme is approximately 6 days [251]. Cell swelling stimulates release of sorbitol [274–276] presumably through channels inserted into the cell membrane by fusion of vesicles [182].

Myoinositol (inositol) [205, 277–280], betaine [281, 282], and taurine [283] are taken up into cells by distinct basolateral Na^+-coupled transport systems. Increased cellular ionic strength [178, 284] but not urea [285] stimulates the transcription of the transporters and thus cellular inositol [281, 286], betaine [281, 285, 287, 288], and taurine [289, 290] accumulation. Betaine may also be accumulated by choline oxidation [291, 292]. Following cell swelling, sorbitol [293], betaine [293], and taurine [289, 290, 294–302] are rapidly released, presumably through channels in the cell membrane (see above).

Besides taurine a variety of other amino acids and amino acid metabolites are modified by changes in cell volume including glutamine, glutamate, glycine, proline, serine, threonine, β-alanine, (n-acetyl)aspartate, and GABA (table 4). The intracellular concentration of most individual amino acids is low. However, the sum of all amino acids significantly contributes to cellular osmolarity in cells exposed to isotonic extracellular fluid [184, 303, 304]. Osmotic cell shrinkage stimulates Na^+-coupled transport of neutral amino acids [305–308]. Furthermore, cell shrinkage stimulates proteolysis [309, 310] and inhibits protein synthesis [311]. Conversely, cell swelling inhibits proteolysis, stimulates protein synthesis [309–312], enhances breakdown of glutamine and glycine [51, 313] and triggers cellular release of several amino acids [58, 294]. As a result, the cellular amino acid concentration increases upon cell shrinkage and decreases upon cell swelling [184].

A number of other metabolites moderately contribute to cellular osmolarity and to the adjustment of cellular osmolarity during alterations of cell volume. Cell swelling increases glycogen synthesis and inhibits glycolysis, thus decreasing the concentration of carbohydrate metabolites [54, 313–321]. In addition, cell swelling slightly stimulates lipogenesis [322]. These effects are, however, only of minor influence on intracellular osmolarity.

Table 4. Osmolytes (figures are reference numbers)

Sorbitol

Erythrocytes 852
Renal medulla 175, 193, 195, 207, 238, 239, 253, 257, 271, 273, 275, 286, 293, 824, 853–875
Urinary bladder 876
Lens epithelial cells 877
Retinal pigment epithelium 879, 880
Astrocytes 881
Vascular smooth muscle cells 882
Renal mesangial cells 883

(Myo)inositol

Skate erythrocytes 884
Renal medulla 175, 193, 195, 207, 238, 239, 286, 293, 853, 862, 867–870, 873–875, 885–890
MDCK cells 281, 779, 891–895
Urinary bladder 876
Glial cells 59, 896–903
Neurons, brain 52, 220, 222, 227, 901, 904–916
Renal mesangial cells 883

Trimethyloxamine

Shark rectal gland 917

Phosphoethanolamine

Brain 222

Glycerophosphorylcholine

Renal medulla 175, 193, 195, 238, 239, 252, 287, 293, 853, 862–865, 867–870, 872, 873, 875, 918–924
MDCK cells 891, 925
Urinary bladder 876
Neurons 220, 227, 913
Renal mesangial cells 883

Choline

Eel erythrocytes 926

Betaine

Skate erythrocytes 884
Renal cortex 927
Renal medulla 175, 193, 195, 207, 238, 239, 285, 287, 293, 853, 862–865, 869, 870, 872–874, 928–934
MDCK cells 282, 284, 779, 893, 935, 936
Brain 937
Shark rectal gland 917
Fibroblasts 310, 938
Mollusc neurons 939
Embryonic cells 940, 941
Mouse macrophages 942, 943
Liver macrophages 944

Taurine

Molluscan erythrocytes 818
Fish erythrocytes 60, 102, 103, 884, 945–951
Avian erythrocytes 952
Lymphocytes 953
Kidney 238, 239, 283, 862–865, 954
Renal medullary cells 382, 867, 887
MDCK cells 61, 283, 289, 290, 392, 955–958
LLC-PK1 cells 955, 958
Trachea 959
Intestine 283
Retina pigment epithelium 710
Retina 300
Lens epithelium 710, 960
Human carcinoma cell line 961, 962
Bovine chondrocytes 963
Placenta 964
Mammary tissue 965
Blastocysts 966
Oocytes 967
HeLa cells 968, 969
Liver 283, 436, 970, 971
Skate hepatocytes 450, 972, 973
Shark rectal gland 917
Molluscan integument 974
Ehrlich ascites tumor cells 294–299, 356
Astrocytes 301, 523, 830, 881, 975–985
Glioma cells 59, 899, 896
Retinal Müller cells 987, 988
Neurons, brain 216, 218, 220, 222, 227, 283, 302, 528, 531, 814, 910, 913, 914, 989–1003
Cardiac cells 283, 1004, 1005
Several tissues of fish 814, 948, 972, 1006–1014

Other amino acids and derivatives (glutamine, glutamate, (n-acetyl)aspartate, GABA, (β)alanine, glycine, serine, proline, threonine)

Fish erythrocytes 926, 1015, 1016
Kidney medulla 184, 862, 873, 1017–1021
MDCK cells 61, 392, 957, 1022
A6 cells 1023
Colonic cells 427, 428
Mammary tissue 965
Lung cancer cells 961

Table 4 (continued)

HeLa cells 968, 969	Skeletal muscle 1025
Astrocytes 523, 978	Skate muscle 1026
Glioma cells 986, 1024	Fibroblasts 303
Neurons 52, 220, 222, 227, 525, 529, 847, 913, 914, 989, 996, 997	Mouse embryo 1027
Heart 989, 1004	**(Phospho)creatine**
Vascular smooth muscle cells 305	Neurons 220, 222, 227, 914

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