Rawyler, A; Arpagaus, S; Brändle, R
Impact of oxygen stress and energy availability on membrane stability of plant cells
Acorus calamus L.; energy shortage; free fatty acids; lipid peroxidation; lipolytic acyl hydrolase; lipoxygenase; membrane intactness; N-acylphosphatidylethanolamine; O(2) stress; reactive oxygen species; Solanum tuberosum L.
This article reviews the relationship between the energy status of plant cells under O(2) stress (e.g. waterlogging) and the maintenance of membrane intactness. using information largely derived from suspension cultures of anoxia-intolerant potato cells. Energy-related parameters measured were fermentation end-products (ethanol, lactate, alanine), respiratory rate, ATP, adenylate energy charge. nitrate reductase activity and biomass. ATP synthesis rates were calculated from the first four parameters, Reactive oxygen species were estimated from H(2)O(2) and superoxide levels, and the enzymatic detoxification potential from the activity levels of catalase and superoxide dismutase. Structure-related parameters were total fatty acids, free fatty acids (FFAs), lipid hydroperoxides, total phospholipids, N-acylphosphatidylethanolamine (NAPE) and cell viability. The following issues are addressed in this review: (1) what is the impact of anoxia on membrane lipids and how does this relate to energy status: (2) does O(2) Per Se play a role in these changes; (3) under which conditions and to what extent does lipid peroxidation occur upon re-aeration and (4) can the effects of re-aeration be distinguished from those of anoxia? The emerging picture is a reappraisal of the relative contributions of anoxia and re-aeration. Two successive phases (pre-lytic and lytic) characterize potato cells under anoxia, They are connected by a threshold in ATP production rate, below which membrane lipids are hydrolysed to FFAs, and NAPE increases. Since lipid peroxidation occurs only when cells are reoxygenated during the lytic phase, its biological relevance in an already damaged system is questionable. (C) 2002 Annals of Botany Company.
ANNALS OF BOTANY 90 (4): 499 - 507, DOI: 10.1093/aob/mcf126, OCT 2002

Kolb, RM; Rawyler, A; Brändle, R
Parameters affecting the early seedling development of four neotropical trees under oxygen deprivation stress
adenylate levels; energy shortage; fermentation capacity; flooding resistance; habitat zonation; lipid hydrolysis; metabolism; seed reserves; Erythrina speciosa; Schizolobium parahyba; Sebastiania commersoniana; Sesbania virgata
Some of the parameters that determine flooding resistance-and consequently habitat zonation-were investigated in four neotropical trees (Schizolobium parahyba, Sebastiania commersoniana, Erythrina speciosa and Sesbania virgata). The constitutive parameters of seeds (size, nature and amount of reserves) only partly influenced resistance to flooding, mainly through a high carbohydrate : size ratio. Parameters describing metabolic efficiency under stress conditions were more important. Among them, fermentation capacity and levels of ATP and of total adenylates played a key role. The highest resistance to anoxia was associated with increased availability of free sugars, elevated alcohol dehydrogenase activity and corresponding mRNA levels, more efficient removal of ethanol and lactate, and higher adenylate levels. Finally, as a lethal consequence of energy shortage, free fatty acids were released on a massive scale in the flooding-sensitive species Schizolobium parahyba, whereas lipid hydrolysis did not occur in the most resistant species Sesbania virgata. (C) 2002 Annals of Botany Company.
ANNALS OF BOTANY 89 (5): 551 - 558, DOI: 10.1093/aob/mcf092, MAY 2002

Arpagaus, S; Rawyler, A; Brändle, R
Occurrence and characteristics of the mitochondrial permeability transition in plants
dThe behavior of purified potato mitochondria toward the main effectors of the animal mitochondrial permeability transition has been studied by light scattering, fluorescence, SDS-polyacrylamide gel electrophoresis, and immunoblotting techniques. The addition of Ca2+ induces a

phosphate-dependent swelling that is fully inhibited by cyclosporin A if dithioerythritol is present. Mg2+ cannot be substituted for Ca2+ but competes with it. Disruption of the outer membrane and release of several proteins, including cytochrome c, occur upon completion of swelling. Ca2+-induced swelling is delayed and its rate is decreased when pH is shifted from 7.4 to 6.6. It is accelerated by diamide, phenylarsine oxide, and linolenic acid. In the absence of Ca2+, however, linolenic acid (less than or equal to20 mum) rapidly dissipates the succinate-driven membrane potential while having no effect on mitochondrial volume. Anoxic conditions favor in vitro swelling and the concomitant release of cytochrome c and of other proteins in a pH-dependent way. These data indicate that the classical mitochondrial permeability transition occurs also in plants. This may have important implications for our understanding of cell stress and death processes.
JOURNAL OF BIOLOGICAL CHEMISTRY 277 (3): 1780 - 1787, DOI: 10.1074/jbc.M109416200, Jan 18 2002

Rawyler, AJ; Brändle, RA
N-acylphosphatidylethanolamine accumulation in potato cells upon energy shortage caused by anoxia or respiratory inhibitors
A minor phospholipid was isolated from potato (Solanum tuberosum L. ev Bintje) cells, chromatographically purified, and identified by electrospray ionization mass spectrometry as N-acylphosphatidylethanolamine (NAPE). The NAPE level was low in unstressed cells (13 +/- 4 nmol g fresh weight(-1)). According to acyl chain length, only 16/18/18 species (group II) and 18/18/18 species (group III) were present. NAPE increased up to 13-fold in anoxia-stressed cells, but only when free fatty acids (FFAs) started being released, after about 10 h of treatment. The level of groups II and III was increased by unspecific N-acylation of phosphatidylethanolamine, and new 16/16/18 species (group 1) appeared via N-palmitoylation. NAPE also accumulated in aerated cells treated with NaN3 plus salicylhydroxamate. N-acyl patterns of NAPE were dominated by 18:1, 18:2, and 16:0, but never reflected the FFA composition. Moreover, they did not change greatly after the treatments, in contrast with O-acyl patterns. Anoxia-induced NAPE accumulation is rooted in the metabolic homeostasis failure due to energy deprivation, but not in the absence of O-2, and is part of an oncotic death process. The acyl composition of basal and stress-induced NAPE suggests the existence of spatially distinct FFA and phosphatidylethanolamine pools. It reflects the specificity of NAPE synthase, the acyl composition, localization and availability of substrates, which are intrinsic cell properties, but has no predictive value as to the type of stress imposed. Whether NAPE has a physiological role depends on the cell being still alive and its compartmentation maintained during the stress period.
PLANT PHYSIOLOGY 127 (1): 240 - 251, DOI: 10.1104/pp.127.1.240, SEP 2001

Pavelic, D; Arpagaus, S; Rawyler, A; Brändle, R
Impact of post-anoxia stress on membrane lipids of anoxia-pretreated potato cells. A re-appraisal
The importance of lipid peroxidation and its contributing pathways (via reactive oxygen species and lipoxygenase) during post-anoxia was evaluated with respect to the biphasic behavior of membrane lipids under anoxia (A. Rawyler, D. Pavelic, C. Gianinazzi, J. Oberson, R. Brändle [1999] Plant Physiol 120: 293-300), using potato (Solanum tuberosum cv Bintje) cell cultures. When anoxic cells in the pre-lytic phase were re-oxygenated for 2 h, superoxide anion was not detectable, the hydrogen peroxide (H2O2) level remained small and similar to that of controls, and cell viability was presented. Lipids were intact and no lipid hydroperoxides were detected. However, small amounts of lipid hydroperoxides accumulated upon feeding anoxic cells with H2O2 and incubation for an additional 2 h under anoxia. When cells that entered the lytic phase of anoxia were re-oxygenated for 2 h, the H2O2 and superoxide anion levels were essentially unchanged. However, cell respiration decreased, reflecting the extensive lipid hydrolysis that had already started under anoxia and continued during post-anoxia. Simultaneous with the massive release of free polyunsaturated fatty acids, small

amounts of lipid hydroperoxides were formed, reaching 1% to 2%; of total fatty acids. Catalase and superoxide dismutase activities were not greatly affected, whereas the amount and activity of lipoxygenase tended to increase during anoxia. Lipid peroxidation in potato cells is therefore low during post-anoxia. It is mainly due to lipoxygenase, whereas the contribution of reactive oxygen species is negligible. But above all, it is a late event that occurs only when irreversible damage is already caused by the anoxia-triggered lipid hydrolysis.
PLANT PHYSIOLOGY 124 (3): 1285 - 1292, DOI: 10.1104/pp.124.3.1285, NOV 2000

Arpagaus, S; Brändle, R
The significance of alpha-amylase under anoxia stress in tolerant rhizomes (Acorus calamus L.) and non-tolerant tubers (Solanum tuberosum L., var. Desiree)
alpha-amylase; anoxia; starch mobilization; translational control
Rhizomes of Acorus calamus L. were able to maintain a functional alpha -amylase under anoxia, whereas a steep decrease in the enzyme protein content and activity took place in potato tubers. The stress-induced control in tubers occurred on the translational level. It is suggested that this decrease is one of the key factors with regard to anoxia intolerance.
JOURNAL OF EXPERIMENTAL BOTANY 51 (349): 1475 - 1477, DOI: 10.1093/jexbot/51.349.1475, AUG 2000

Oberson, J; Pavelic, D; Brändle, R; Rawyler, A
Nitrate increases membrane stability of potato cells under anoxia
Solanum tuberosum L.; anoxia; energy status; fatty acids; lipid hydrolysis; nitrate; nitrate reductase; nitrite; potato cells
Potato cells (Solanum tuberosum L.), cultivated in original Murashige-Skoog (MS) medium for 5 days were subsequently transferred into MS media containing nitrate or ammonium as sole inorganic N source and incubated under anoxia for 24 h. With regard to lipid stability these cells behaved differently Although lipid hydrolysis occurred in both cases by the same mechanism, nitrate was able to postpone free fatty acid release for about 6 h compared with ammonium within the 24 h anoxia treatment. The increased membrane lipid stability of nitrate-treated cells under anoxia was correlated with a higher nitrate reduction capability and an improved energy status.
JOURNAL OF PLANT PHYSIOLOGY 155 (6): 792 - 794, DEC 1999

Rawyler, A; Pavelic, D; Gianinazzi, C; Oberson, J; Brändle, R
Membrane lipid integrity relies on a threshold of ATP production rate in potato cell cultures submitted to anoxia
In this paper we report on our study of the changes in biomass, lipid composition, and fermentation end products, as well as in the ATP level and synthesis rate in cultivated potato (Solanum tuberosum) cells submitted to anoxia stress. During the first phase of about 12 h, cells coped with the reduced energy supply brought about by fermentation and their membrane lipids remained intact. The second phase (12-24 h), during which the energy supply dropped down to 1% to 2% of its maximal theoretical normoxic value, was characterized by an extensive hydrolysis of membrane lipids to free fatty acids. This autolytic process was ascribed to the activation of a lipolytic acyl hydrolase. Cells were also treated under normoxia with inhibitors known to interfere with energy metabolism. Carbonyl-cyanide-4-trifluoromethoxyphenylhydrazone did not induce lipid hydrolysis, which was also the case when sodium azide or salicylhydroxamic acid were fed separately. However, the simultaneous use of sodium azide plus salicylhydroxamic acid or 2-deoxy-D-glucose plus iodoacetate with normoxic cells promoted a lipid hydrolysis pattern similar to that seen in anoxic cells. Therefore, a threshold exists in the rate of ATP synthesis (approximately 10 mu mol g(-1) fresh weight h(-1)), below which the integrity of the membranes in anoxic potato cells cannot be preserved.
PLANT PHYSIOLOGY 120 (1): 293 - 300, DOI: 10.1104/pp.120.1.293, MAY 1999

Oberson, J; Rawyler, A; Brändle, R; Canevascini, G
Analysis of the heat-shock response displayed by two Chaetomium species originating from different thermal environments
Chaetomium thermophile; fungal thermophily; heat shock protein; trehalose; fatty acid composition; 2D-PAGE
Three features of the heat shock response, reorganization of protein expression, intracellular accumulation of trehalose, and alteration in unsaturation degree of fatty acids were investigated in the thermophilic fungus Chaetomium thermophile and compared to the response displayed by a closely related mesophilic species, C, brasiliense. Thermophilic heat shock response paralleled the mesophilic response in many respects like (i) the temperature difference observed between normothermia and the upper limit of translational activity, (ii) the transient nature of the heat shock response at the level of protein expression including both the induction of heat shock proteins (HSPs) as well as the repression of housekeeping proteins, (iii) the presence of representatives of high-molecular-weight HSPs families, (iv) intracellular accumulation of trehalose, and finally (v) modifications in fatty acid composition. On the other hand, a great variability between the two organisms was observed for the proteins expressed during stress, in particular a protein of the HSP60 family that was only observed in C. thermophile. This peptide was also present constitutively at normal temperature and may thus fulfil thermophilic functions. It is shown that accumulation of trehalose does not play a part in thermophily but is only a stress response. C, thermophile contains less polyunsaturated fatty acids at normal temperature than C, brasiliense, a fact that can be directly related to thermophily When subjected to heat stress, both organisms tended to accumulate shorter and less unsaturated fatty acids. (C) 1999 Academic Press.
FUNGAL GENETICS AND BIOLOGY 26 (3): 178 - 189, DOI: 10.1006/fgbi.1999.1116, APR 1999

Tadege, M; Brändle, R; Kuhlemeier, C
Anoxia tolerance in tobacco roots: effect of overexpression of pyruvate decarboxylase
Plant survival during flooding relies on ethanolic fermentation for energy production. The available literature indicates that the first enzyme of the ethanolic fermentation pathway, pyruvate decarboxylase (PDC), is expressed at very low levels and is likely to be rate-limiting during oxygen deprivation. The authors expressed high levels of bacterial PDC in tobacco to study the modulation of PDC activity in vivo, and assess its impact on the physiology of ethanolic fermentation and survival under oxygen stress. In contrast to leaves, wild-type normoxic roots contained considerable PDC activity, and overexpression of the bacterial PDC caused only a moderate increase in acetaldehyde and ethanol production under anoxia compared to wild type roots. No significant lactate production could be measured at any time, making it unlikely that lactate-induced acidification (LDH/PDC pH-stat) triggers the onset of ethanol synthesis. Instead, the authors favour a model in which the flux through the pathway is regulated by substrate availability The increased ethanolic flux in the transgenics compared to the wild-type did not enhance anoxia tolerance. On the contrary, rapid utilisation of carbohydrate reserves enhanced premature cell death in the transgenics while replenishment of carbohydrates improved survival under anoxia.
PLANT JOURNAL 14 (3): 327 - 335, DOI: 10.1046/j.1365-313X.1998.00130.x, MAY 1998

Crawford, RMM; Brändle, R
Oxygen deprivation stress in a changing environment
anoxia; hypoxia; flooding; Zea mays; Solanum tuberosum; Oryza sativa; Acorus calamus; Phragmites australis; Glyceria maxima; cranberry
Past research into flooding tolerance and oxygen shortages in plants has been motivated largely by cultivation problems of arable crops. Unfortunately, such species are unsuitable for investigating the physiological and biochemical basis of anoxia-tolerance as selection has reduced any tolerance of anaerobiosis and anaerobic soil conditions that their wild ancestors might have possessed,

Restoration of anoxia-tolerance to species that have lost this property is served better by physiological and molecular studies of the mechanisms that are employed in wild species that still possess long-term anoxia-tolerance. Case studies developing these arguments are presented in relation to a selection of crop and wild species, The flooding sensitivity and metabolism of maize is compared in relation to rice in its capacity for anaerobic germination, The sensitivity of potato to flooding is related to its disturbed energy metabolism and inability to maintain functioning membranes under anoxia and post-inoxia, By contrast, long-term anoxia-tolerance in the American cranberry (Vaccinium macrocarpon) and the arctic grass species Deschampsia beringensis can be related to the provision and utilization of carbohydrate reserves. Among temperate species, the sweet flag (Acorus calamus) shows a remarkable tolerance of anoxia in both shoots and roots and is also able to mobilize carbohydrate and maintain ATP levels during anoxia as well as preserving membrane lipids against anoxic and post-anoxic injury. Phragmites australis and Spartina alterniflora, although anoxia-tolerant, are both sulphide-sensitive species which can pre-dispose them to the phenomenon of die-back in stagnant, nutrient-rich water. Glyceria maxima adapts to flooding through phenological adaptations with a seasonal metabolic tolerance of anoxia confined to winter and spring which, combined with a facility for root aeration and early spring growth, allows rapid colonization of sites with only shallow flooding. The diversity of responses to flooding in wild plants suggests that, depending on the life strategy and habitat of the species, many different mechanisms may be involved in adapting plants to survive periods of inundation and no one mechanism on its own is adequate for ensuring survival.
JOURNAL OF EXPERIMENTAL BOTANY 47 (295): 145 - 159, DOI: 10.1093/jxb/47.2.145, FEB 1996

Brändle, R; Pokorny, J; Kvet, J; Cizkova, H
Wetland plants as a subject of interdisciplinary research
anoxia; flooding; internal aeration; metabolic adaptations; Phragmites decline
FOLIA GEOBOTANICA & PHYTOTAXONOMICA 31 (1): 1 - 6, DOI: 10.1007/BF02803989, 1996

Weber, M; Brändle, R
Some aspects of the extreme anoxia tolerance of the sweet flag, Acorus calamus L.
ammonia; energy metabolism; fermentation; macromolecule synthesis; membrane stability; oxygen deprivation; sulphide
Acorus calamus L. is a neophyte in Europe with remarkable properties. Among other things, it is the most anoxia tolerant species and a competitive invader at eutrophic sites. The following overview presents the most recent work on these subjects. Carbohydrates of the rhizomes sustain anaerobic ATP production for very long periods. Ethanolic fermentation naturally occurs in winter and produces rather low, but sufficient amounts of ATP for survival, as shown by adenylate energy charge and total adenylate content. Fermentation energy is mainly used for the synthesis and preservation of essential macromolecules, such as proteins and membrane lipids. The extent of these processes is unique. Moreover, ammonia and sulphide uptake is maintained during the cold season. Both ions are detoxified to alanine and thiols which are translocated into the rhizome, where the nitrogen of alanine is used to form arginine. Overwintering leaves contain asparagine instead of arginine. Recycled nitrogen compounds from the rapidly degrading summer leaves return into the rhizomes. Therefore, the nitrogen nutrition consists of an external and internal cycle. The abundance of carbohydrates and nitrogen compounds allows spring shoot growth earlier than other species. These strategies could contribute markedly to the competitive power of A. calamus at its natural site.
FOLIA GEOBOTANICA & PHYTOTAXONOMICA 31 (1): 37 - 46, DOI: 10.1007/BF02803992, 1996

Furtig, K; Ruegsegger, A; Brunold, C; Brändle, R
Sulphide utilization and injuries in hypoxic roots and rhizomes of common reed (Phragmites australis)
adenylates; detoxification; energy metabolism; glutathione; thiols; viability

The presented investigations have been carried out in order to estimate toxic sulphide levels and to examine detoxification capabilities in roots and rhizomes of the common reed (Phragmites australis). Underground organs of common reed are sensitive towards sulphide above 1 mM applied exogenously under hypoxia. However, certain tolerance may be achieved by sulphide detoxification. Accumulated sulphide is partially used for the synthesis of npn-toxic thiols, mainly glutathione: But the detoxification capacity of the fw in roots and 300 underground organs is limited. Maximum concentrations of thiols are about 60 nmol/g(-1) nmol/g(-1) fw in rhizomes. Energy metabolism is considerably affected by low sulphide concentrations of 1 mM for 4 days, and immediately disturbed by increased concentrations up to 6 mM sulphide. Adenylate energy charge, total adenylates, posthypoxic respiration, and fermentation capacity decrease significantly. Roots are more sensitive than rhizomes.
FOLIA GEOBOTANICA & PHYTOTAXONOMICA 31 (1): 143 - 151, DOI: 10.1007/BF02804003, 1996

Bucher, M; Brändle, R; Kuhlemeier, C
Glycolytic gene expression in amphibious Acorus calamus L under natural conditions
cold acclimation; ecophysiology; fermentation; flooding; gene expression
Acorus calamus L is an amphibious plant, which is exposed to periods of flooding and consequently hypoxic conditions as a part of its natural life cycle. Previous experiments under laboratory conditions have shown that the plant can survive for two months in the complete absence of oxygen, and that during this period the expression of genes encoding the glycolytic enzymes fructose-1,6-bisphosphate aldolase (ALD), pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) is induced in leaves and rhizomes (Bucher and Kuhlemeier, 1993). Here we studied the expression of ALD and ADH through two years in the natural habitat of A, calamus. Under natural conditions roots and rhizomes were always submerged but newly grown leaves emerged in spring; in autumn the leaves senesced and the whole plant was submerged again. High Aid and Adh mRNA levels in leaf and rhizome were found only in winter when the leaves were entirely submerged. Upon leaf emergence in spring the mRNA levels rapidly declined. Under controlled experimental conditions expression of Aid and Adh was not induced by low temperature. The combination of laboratory and field experiments supports the hypothesis that oxygen deprivation rather than low temperature is a major regulator of glycolytic gene expression in A. calamus. The possible role of other environmental factors is also discussed.
PLANT AND SOIL 178 (1): 75 - 82, DOI: 10.1007/BF00011165, JAN 1996

SCHAFFNER, U; NENTWIG, W; BRÄNDLE, R
EFFECT OF MOWING, RUST INFECTION AND SEED PRODUCTION UPON C-RESERVES AND N-RESERVES AND MORPHOLOGY OF THE PERENNIAL VERATRUM-ALBUM L (LILIALES, MELANTHIACEAE)
VERATRUM ALBUM; NITROGEN CARBOHYDRATE RESERVES; MOWING; SEED PRODUCTION; FUNGAL INFECTION
In this field study the effect of mowing, rust infection and seed production was determined on nonstructural carbohydrate (C) and Kjeldahl nitrogen (N) reserves in rhizomes, as well as on plant morphology of the perennial weed Veratrum album L. (Liliales, Melanthiaceae). Rust infection and seed production had only a minimal influence on the concentrations of C and of N during either the summer or the following winter. However, mowing one month after early shoot growth led to decreased C (-40%) and increased N (+100%) concentrations of rhizomes sampled during the following winter. In a long-term experiment, the decrease in C reserves was shown to coincide with dwarfism of V. album plants. Mowing for six consecutive years reduced total plant biomass by 50%. Accordingly, total N and C reserves per plant rhizome decrease substantially. However, seasonal patterns of C and N concentrations were not influenced by mowing, except for the differences in winter concentrations that were already observed in the Short-term experiment. Long-time mowing not only led to dwarfism of V. album plants, but also significantly decreased generative and

vegetative proliferation.
BOTANICA HELVETICA 105 (1): 17 - 23, JUL 1995

JOLY, CA; BRÄNDLE, R
FERMENTATION AND ADENYLATE METABOLISM OF HEDYCHIUM-CORONARIUM KOENIG,J.G. (ZINGIBERACEAE) AND ACORUS-CALAMUS L (ARACEAE) UNDER HYPOXIA AND ANOXIA
ADENYLATE ENERGY CHARGE; ANAEROBIC METABOLISM; WATERLOGGING
1. Rhizomes of wetland plants are subjected to periods of hypoxia and/or anoxia by the seasonal or permanent waterlogging of their growing sites. Hedychium coronarium, the White Ginger, and Acorus calamus, the Sweet Flag, have their origin in India and were introduced into Latin America and Europe, respectively, more than three centuries ago. The White Ginger grows in humus-rich, shaded or semi-shaded areas subjected to waterlogging but it is never totally submersed, while the Sweet Flag grows at lake margins and is totally submersed during winter. 2. Winter rhizomes of both species were cultivated in water culture in a greenhouse. The end products of fermentation (ethanol, lactic acid, malic acid), overall rhizome pH, the adenylate pool of nucleotides, the energy charge and their capacity to resume growth, were measured after periods of 1, 2, 4, 8 and 16 days of anoxia and hypoxia. In all cases metabolic responses were also determined in rhizomes allowed to recover for 24 h in air. 3. Ethanol was the main fermentation end product in both species, reaching higher concentrations in the anoxia-treated rhizomes. In H. coronarium, there was also a significant increase in the levels of lactic acid, with a considerable drop in overall rhizome pH. 4. Anoxia and hypoxia induced, in both species, a significant drop in the energy charge values. Control plant rhizomes and rhizomes allowed to recover in air for 24 h had energy charge values of around 0.8. In rhizomes subjected to stress these values were lower, around 0.50 in A. calamus and as low as 0.3 in H. coronarium. 5. Although in both species there is also a decrease in the amount of total nucleotides, it was much more drastic in the case of anoxia treated rhizomes of H. coronarium. The pH drop was most probably the underlying cause of the metabolic disarray that lead to a depletion of the adenylate pool and, finally, failure to regenerate after 16-days of anoxia. 6. The results also show that energy charge values without measurements of the total adenylate pool may give a misleading impression of fitness. Thus, the anaerobic metabolism of H. coronarium is less efficient and more harmful than that of A. calamus and, although considerably tolerant to hypoxia, it does not tolerate strict anoxia as the latter species does.
FUNCTIONAL ECOLOGY 9 (3): 505 - 510, DOI: 10.2307/2390016, JUN 1995

PfisterSieber, M; Brändle, R
Response of potato tubers to hypoxia followed by re-aeration
adenylate energy charge; fermentation; lipid peroxidation; posthypoxia; Solanum tuberosum L
Potato tubers kept under hypoxia (1%) showed improved viability in comparison to anoxia, which was associated with the maintenance of intermediate adenylate energy charge values (A.E.C. = 0.6) and stable adenylate pools at 50% of the initial levels. Re-admission of oxygen to the tuber resulted in an almost full recovery of adenylate energy charge and total adenylates after up to 3 days of hypoxic pretreatment. Tubers exhibited a mixed fermentation. The high lactate. ethanol and acetaldehyde levels proved to be non toxic. Ethanol was degraded to acetaldehyde during re-aeration. Posthypoxic lipid peroxidation was indicated by malondialdehyde and ethane formation. Both products occurred with a temporary delay and in lower amounts compared to post-anoxia. Ethylene release was also considerably smaller. Severe hypoxia and posthypoxia postponed tissue death compared to anoxia. Survival was correlated with an improved energy supply which stabilized membranes.
POTATO RESEARCH 38 (3): 231 - 239, DOI: 10.1007/BF02359905,  1995

ARMSTRONG, W; BRÄNDLE, R; JACKSON, MB
MECHANISMS OF FLOOD TOLERANCE IN PLANTS
FLOODING; SUBMERGENCE; ENVIRONMENTAL STRESS; PLANT HORMONES; ADAPTATION; REVIEW
ACTA BOTANICA NEERLANDICA 43 (4): 307 - 358, DEC 1994

BUCHER, M; BRÄNDLE, R; KUHLEMEIER, C
ETHANOLIC FERMENTATION IN TRANSGENIC TOBACCO EXPRESSING ZYMOMONAS-MOBILIS PYRUVATE DECARBOXYLASE
AEROBIC FERMENTATION; ALCOHOL DEHYDROGENASE GENE EXPRESSION; ANOXIA; TRANSGENIC TOBACCO; ZYMOMONAS MOBILIS PYRUVATE DECARBOXYLASE
During oxygen limitation in higher plants, energy metabolism switches from respiration to fermentation. As part of this anaerobic response the expression of genes encoding pyruvate decarboxylase (PDC) and alcohol dehydrogenase (ADH) is strongly induced. In addition there-is ample evidence for post-translational regulation. In order to understand this multi-level regulation of the anaerobic response, we provided tobacco with the constitutive capacity of ethanolic fermentation by expressing a PDC gene derived from the obligate anaerobe Zymomonas mobilis. The protein accumulated to high levels and was active in an in vitro assay. During the first 2-4 h of anoxia, acetaldehyde accumulated to 10- to 35-fold and ethanol to 8- to 20-fold higher levels than in wild-type. Under normoxic conditions no accumulation of acetaldehyde and ethanol could be measured. Instead, the two products may be immediately re-metabolized in tobacco leaf tissue. We show that aerobic fermentation takes place when the respiratory system is inhibited. Although these conditions enhance ethanolic fermentation under normoxia, they fail to increase ADH transcript levels. These results indicate that anaerobic transcription is triggered not by the metabolic consequences of oxygen limitation, but directly through an oxygen-sensing system.
EMBO JOURNAL 13 (12): 2755 - 2763, Jun 15 1994

WEBER, M; BRÄNDLE, R
DYNAMICS OF NITROGEN-RICH COMPOUNDS IN ROOTS, RHIZOMES, AND LEAVES OF THE SWEET FLAG (ACORUS-CALAMUS L) AT ITS NATURAL SITE
ACORUS-CALAMUS L; ALANINE; ARGININE; ASPARAGINE; BLEEDING SAP; NITROGEN CYCLING
The seasonal dynamics of nitrogen reserve compounds depends not only on the climatic factors but also on the special behaviour of the sweet flag (Acorus calamus L.). It bears green submersed non-growing leaves in winter and leaf extension occurs earlier than that of surrounding plants in spring. Roots, rhizomes and leaves are not of equal importance with respect to nitrogen storage. Because of its high biomass, most nitrogen is stored in the rhizome. Leaves show similar concentrations of nitrogen but the biomass in winter is considerably lower. Roots are storage organs of minor importance, yet they survive winter. These organs differ in the kind of nitrogen compounds they contain. In the rhizome, high amounts of arginine, asparagine and proteins are present in winter. Asparagine is the predominant amino acid in winter leaves. Alanine accumulates in roots when plants are submerged. Concentrations of ammonium are moderate throughout the year in roots (1 - 2 mumol/g fw). Arginine seems not to be translocated in large amounts out of the rhizome into expanding leaves. Analysis of bleeding sap showed hardly any arginine but elevated concentrations of asparagine and glutamine. With respect to nitrogen cycling strategies, we conclude that A. calamus is a combination of the translocation type and the assimilation type. Nitrogen compounds of senescing leaves are efficiently translocated into rhizomes. Furthermore, ammonium is available throughout the whole year and is used to form amino acids. The significance of these and other facts is discussed with regard to this plants success as a vigorous invader at its site.
FLORA 189 (1): 63 - 68, MAR 1994

PFISTERSIEBER, M; BRÄNDLE, R
ASPECTS OF PLANT BEHAVIOR UNDER ANOXIA AND POSTANOXIA
All plants are able to survive anoxic periods, but the degree of tolerance shows large variation. The main injuries related to anoxia are eventually due to changes in energy metabolism. Low energy charge values indicate a cessation of many ATP consuming processes. Sugar starvation, lactic acid fermentation and proton release from leaky vacuoles are responsible for cell death. Long-term anoxia tolerance is dependent on storage products in the vicinity of sinks, on an adequate control of glycolysis, synthesis of essential proteins, and stability of membranes and organelles. However, no fundamental differences between the metabolic pathways of tolerant and non-tolerant tissues are known. It is rather a question of minor changes and the regulation of anaerobic metabolism. Re-exposure of anoxic tissues to air may even be more detrimental than anoxia itself. These injuries are mainly due to enhanced radical generation. Lipid peroxidation processes lead to membrane damage, disintegration, and leakage of solutes. Under natural conditions plants are equipped with radical-detoxifying systems (SOD, peroxidases and antioxidants). Natural detoxifying systems can be reduced in non-adapted plants under anoxia and they become more sensitive to post-anoxic damage. In addition, the rapid conversion of ethanol to extremely toxic acetaldehyde seems to be a cause of tissue injury and death.
PROCEEDINGS OF THE ROYAL SOCIETY OF EDINBURGH SECTION B-BIOLOGICAL SCIENCES 102 (): 313 - 324, 1994

SIEBER, M; BRÄNDLE, R
ENERGY-METABOLISM IN RHIZOMES OF ACORUS-CALAMUS (L) AND IN TUBERS OF SOLANUM-TUBEROSUM (L) WITH REGARD TO THEIR ANOXIA TOLERANCE
ACORUS-CALAMUS; ADENYLATE ENERGY CHARGE; ANOXIA; FERMENTATION; SOLANUM-TUBEROSUM
Rhizomes of the marsh plant Acorus calamus (L.) and tubers of the flooding-intolerant Solanum tuberosum (L.) var. Bintje, both kept under strict anoxia, differ markedly in their fermentation properties. The fermentation capacities as measured by ADH and LDH activities and their respective product concentrations were estimated. While rhizomes of Acorus calamus, having high ADH and low LDH activities, accumulate mainly ethanol, tubers of Solanum tuberosum tend towards lactic acid fermentation. The total amount of adenine nucleotides is quite stable in Acorus calamus, whereas they show a sharp decline in S. tuberosum during the first 6 h of anoxia. The adenylate energy charge of A. calamus recovers after a short initial drop (AEC > 0.8). AEC values of S. tuberosum decrease rapidly and remain at very low values (AEC approximately 0.3). Tuber tissues became soft and lost viability after about 48-72 h of anoxia at 25-degrees-C. This might be due to tissue acidification and impaired energy metabolism, but not to the lack of energy reserves. Energy metabolism of A. calamus is well adapted to anoxia.
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ETHYLENE-DEPENDENT GROWTH AND DEVELOPMENT OF CUTTINGS OF THE WATERCRESS (NASTURTIUM-OFFICINALE R BR)
ETHYLENE; FLOODING; DEVELOPMENT; GROWTH; NASTURTIUM-OFFICINALE; SUBMERGENCE; WATERCRESS
Ethylene promotes shoot formation from buds and restricts adventitous root formation in cuttings of the water cress. The ethylene effects are counteracted by silver ions but not by cobalt ions in the presence of ethylene. Flooding or submergence of cuttings mimics the ethylene mediated growth processes. The internal atmosphere of submerged plant tissues is enriched in ethylene. Despite the limited development of the adventitous root system, plantlets regenerate to independent plants within a few days. This behaviour can be interpreted as an adaptive strategy to periodical flooding as

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