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Thermodynamics of Seed and Plant Growth

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1. Introduction

Living systems are open, irreversible systems, determined by inheritance and dependent on temperature and time. They exchange substances with the environment and they need free energy for life. Living systems transform energy and matter during metabolism, which could be described as a controlled capacity to transform energy, by the First Law of Thermodynamics. Nevertheless, energy transformation includes the loss of some free energy as heat, by the Second Law of Thermodynamics, which as a consequence increases disorder - entropy. Plant cells are simultaneously characterized by two opposing types of reactions: endergonic, such as photosynthesis (occurring in green plastids) and exergonic, such as respiration (present in mitochondria). Since the metabolic reactions are controlled, they need activation energy that is provided by biological catalysts - enzymes, which lower the activation energy without its consumption. Nevertheless, the limits in the application of thermodynamics in the biochemistry of living systems are the non-existence of time and total reversibility, as a category, which could be surpassed in plant systems by introducing of temperature sums as important factor of plant development.

A living system assimilates high-enthalpy, low-entropy compounds from its surroundings, transforms them into a more useful form of chemical energy and returns low-enthalpy, high-entropy compounds to environment. From this point of view, a living organism must be ordered and cannot be at equilibrium. Steady state in an open system is the analogue of equilibrium in a closed system. From the standpoint of thermodynamics, the normal functions of living systems are enabled by the concomitant presence of two opposing tendencies: the preservation of a steady state and the aspiration to spontaneously transcend a non-equilibrium state. A steady state, *i.e.*, near-equilibrium state is maintained based on minimal energy expenditure (Taiz & Zeiger, 2010). A steady inward flow of energy is the most stable state that an open system can achieve. Furthermore, the last ten years of 20th century were marked by the application of thermodynamics to research of functional (such as erythrocytes) and reproducible (such as *Methylobacterium extorquens*) cell growth (Holzhütter, 2004). In higher plants, the functional and reproducible parts in seed are connected by the irreversible transfer of hydrolysed monomers from an endosperm (functional) to an embryo (reproducible). The product of seed germination - a plant, consists of two reciprocally reversible segments: a root and a shoot, which grow by the simultaneous presence of two processes: cell elongation and cell division. Water plays an important role in growing processes. At the end of the 1960s, Boyer (1969) introduced the energy concept, to quantify water transport into plants. In addition, the input of water was determined as energy input in an essay with seedlings of different crops (Manz et al., 2005; Kikuchi et al., 2006).

Plants are open systems which can directly use (transform) light energy to convert CO_2 and H_2O into glucose, which cellular respiration converts into ATP. They reproduce and survive the unfavourable conditions in the form of seeds. A seed is a living system with a low water content and metabolism reduced to the minimum. It contains genetic information which enables the life of a new plant. The most critical period for a seed is imbibition and the beginning of germination, which represents a shifting of the system from a latent state (steady state). Seed storage (ageing factor) induces qualitative and quantitative changes, which could have as a consequence loss of viability. If deterioration is not significant, the system results in a new plant by rehydration and substance allocation present in processes of hydrolysis and biosynthesis. During its lifetime cycle, a plant dissipates energy gradients from the point of growth and development. Environmental stresses increase the internal entropy of a plant, moving it closer to equilibrium. In response, plants employ repair systems, requiring additional energy for the recovery processes, having as a consequence a lowering of the energy available for work and an increase in entropy. Decrease of entropy of any living system towards equilibrium, having as a consequence death (Shimokawa & Ozawa, 2005).

2. The thermodynamics of seed and the maintenance of seed viability

A seed is a biological system in the state of anhydrobiosis with living processes reduced to the minimum to maintain the germination ability (viability) - the crucial biological aspect. The term is derived from Greek and indicates "life without water". Anhydrobiosis is a highly stable state of suspended energy due to desiccation pending recovery by rehydration. This state seems always to be characterized by the cessation of measurable metabolism. From this point, seed viability could be maintained during long periods owing to their glass structure, which was defined by Buitink & Leprince (2004) as a thermodynamically unstable state, with high viscosity (enabled by low tissue moisture and low temperature), so as the viscosity is so high that diffusional movement is effectively prevented for time periods of practical utility. Sun (2000); Walters (2007); Buitink & Leprince (2008) ascertained that glass stability is not upheld *per se*, it is based on groups of different biomolecules, linked by hydrogen bonds with water molecules. Bryant et al. (2001) and Benson (2008) suggested that the formation of a glassy matrix (i.e., vitrification) in could represent a strategy for desiccation tolerance and storage stability, in general. Vitrification achieves a high viscosity without a great deal of molecular reorganization (Hatanaka & Sugawara, 2010) and, therefore, limits major changes in the cellular structures (Buitink & Leprince, 2008; Walters et al., 2010). Glasses exhibit temperature-dependent transitions during which they pass from a glassy mechanical solid to a state with a markedly decreased viscosity. This can be detected by a change in the heat capacity or by direct measurement of mechanical relaxation of viscosity (Walters et al., 2010).

2.1 Seed structure and water as bearer of equilibrium

Water is of great importance for living systems; either it is a reaction medium or a reactant. The main characteristic of seed is low water content, which could vary depending on plant species, environment and seed condition (Beardmore et al., 2008; Siddiqui et al., 2008). Seed water consists of two components, bound and bulk water (Krishnan et al., 2004c).

Ageing is a characteristic of all living systems, seeds included. Irrespective to fact that vitrification presents a conservation state for seed systems (close to a steady state), silent

metabolic processes are present, with a lower ability to counteract developed injuries. This means that vitrification has a double nature: conservation (low entropy and enthalpy) with a low ability of recovery, as opposed to the hydrated state, where the entropy and enthalpy are large with high mobility and high recovery ability.

Based on ability to maintain viability during long periods and to endure desiccation, Pammentner & Berjak (1999) divided the seeds of all plant species into two groups:

1. Orthodox - which could be stored for a long time and endure extreme desiccation;
2. Recalcitrant - which could not be stored for a long time and could be injured by desiccation.

From the point of glass stability, water and temperature play significant roles in determining the storage longevity of orthodox seeds. Some models have demonstrated that the effects of water and temperature on seed aging are interdependent (Beardmore et al., 2008), indicating desiccation as the main contributor to loss of seed viability. On the other hand, Walters et al. (2001; 2010) considered that seed ageing, as the main result of free radical production, is the most important factor for viability loss. Furthermore, Vertucci (1989) established that an increase of seed moisture over 0.25 g g⁻¹ dry weight increases seed respiration. One of the basic mechanisms in energy transmission during desiccation (induced by ageing) is the redox state of system (Kraner & Birtić, 2005). This gives a more complex view to the maintenance of seed viability.

Desiccation of plant tissues presents a shift of the water from the liquid to the vapour phase (Sun, 2002). Temperature influences evaporation, as well as the partial water vapour pressure in the air and the energy status of water in plant tissue, both in dry and hydrated plant tissue. An increase in temperature results in a decrease in the equilibrium water content at a given relative humidity (water activity) or an increase in the equilibrium water activity for a given tissue water content (Fig. 1). Water activity can be described as the 'effective' water content, which is thermodynamically available for various physiological processes in cells. The temperature dependence of the isotherm shift is described by the Clausius-Clapeyron Equation:

$$\ln = \frac{a_{w2}}{a_{w1}} = \frac{q + \lambda_w}{R} = \left[\frac{1}{T_2} - \frac{1}{T_1} \right] \quad (1)$$

where q is the excess heat of sorption; λ_w is the latent heat of vaporization for water (44.0 kJ kg⁻¹ at 25°C); R is the gas constant; a_{w1} and a_{w2} are the water activities for a given equilibrium water content at temperature T_1 and T_2 , respectively.

The structural changes observed during the process of seed ageing consider disturbances of the glass structure (Hoekstra et al., 2001; Walters et al., 2010) and the increase of the oxidative activity (Walters et al., 2001; Dussert et al., 2006) as a consequence of increased respiration. Based on thermodynamics, the change of internal energy of a system represents the maximal work which could be achieved.

The alterations of external (temperature and/or humidity) and internal factors (glass stability) influence the respiration of dry seeds (Walters et al., 2001) and their energy status, which could be calculated by use of the sorption isotherm, as suggested by Vertucci & Leopold (1984):

$$\Delta H = \frac{R T_1 T_2}{T_2 - T_1} \ln \left(\frac{a_{w1}}{a_{w2}} \right) \quad (2)$$

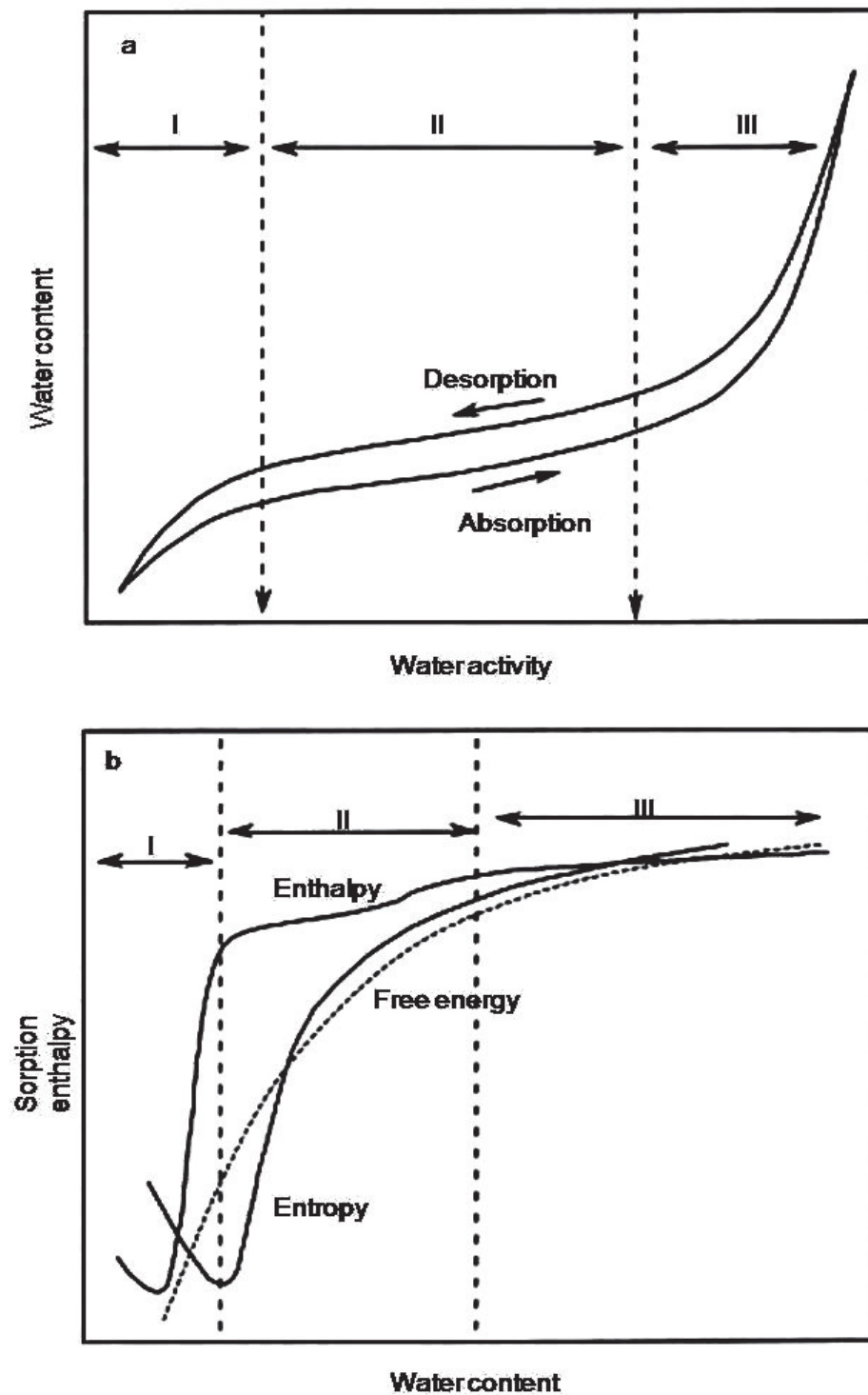


Fig. 1. Analysis of the water sorption isotherms. (a) Typical shapes of the desorption and adsorption curves of plant tissues. The difference between these two curves shows hysteresis, indicating the irreversibility of water sorption in the tissues during dehydration and rehydration. The sigmoid shape of sorption curves is presumably due to the existence of three types of water-binding sites in tissues (strong (I), weak (II) and multilayer molecular sorption sites (III)). (b) Differential enthalpy (ΔH), free energy (ΔG) and entropy (ΔS) of hydration. Data from Sun (2002).

$$\Delta G = RT \ln(a_w) \quad (3)$$

$$\Delta S = \frac{\Delta H - \Delta G}{T} \quad (4)$$

where, at a given tissue water content, a_{w1} and a_{w2} are the relative humidity at the lower and higher temperatures: T_1 and T_2 , respectively, ΔH is the differential enthalpy of hydration, ΔG is the differential free energy and ΔS is the differential entropy, while R is the gas constant ($8.3145 \text{ J mol}^{-1} \text{ K}^{-1}$).

Irrespective of the fact that the observed experiments were performed on tissue during hydration/dehydration, it is well known that even minimal water content in seeds could have an important function in altering the glassy matrix. Molecular mobility was found to be inversely correlated with storage stability. With decreasing water content, the molecular mobility reached a minimum, but increased again at very low water contents. This correlation suggests that storage stability might be at least partially controlled by molecular mobility (Buitink et al., 2000).

Krishnan et al. (2004b) ascertained that the thermodynamic properties of seed water determine the reaction kinetics during seed deterioration. The thermodynamic properties showed a critical upper limit, with tolerant species having higher values than susceptible species. In general, the values of the critical limits of the thermodynamic parameters decreased with increasing temperature. The differential enthalpy and entropy increased in seeds with period of storage and became asymptotic as the seeds lost their viability. The importance of temperature, as a seed deterioration factor was also emphasised by Dragicevic (2007), with the increased values of the differential free energy found during accelerated ageing of susceptible (sugary genotypes) and tolerant (dent genotypes) maize seeds (Fig. 2). The radical increase in the ΔG values indicates intensification of endergonic reactions and consumption of relative high amounts of energy (Davies, 1961; Sun, 2002). It should be mentioned that the observed research data were calculated using temperature sums, which have a significant function in plant development. From this point of view, a time category was introduced in the plant thermodynamics and Gladyshev's (2010) postulate on hierarchical thermodynamics that the thermodynamics of a system considers only the initial and final states (the importance of whether the process under study occurs under equilibrium or non-equilibrium conditions) could be enhanced. Parallel to the results of Krishnan et al. (2004b), the differential ΔS and ΔH increased (Fig. 3) with the period of accelerated ageing. Whereas the entropy presents capacity, which means that the system is holding under conditions of limited energetic capacity and relative stability ($\Delta S \leq 0$), characteristic for seed glasses (Sun, 2002; Walters, 2007; Buitink & Leprince, 2008), in addition, the higher entropy values, present in dent seeds, could indicate a higher capacity of the system to undergo change. Concomitantly, the ΔH values, as a measure of total energy, have sigmoid shapes, with values $\Delta H > 0$ for dent seeds, as tolerant genotypes. Meanwhile, the radical decrease in germination corresponds with the trend of enthalpy decrease, with values present on the negative part of the scale, indicating a shift of the system from a relatively ordered state to a random state (Davies 1961; Sun, 2002). The observed results are in accordance with the data of Krishnan et al. (2004a, 2004b) concerning seeds with a low germination potential, which is characterized by low relaxation, as well as values below the boundary of enthalpy equilibrium.

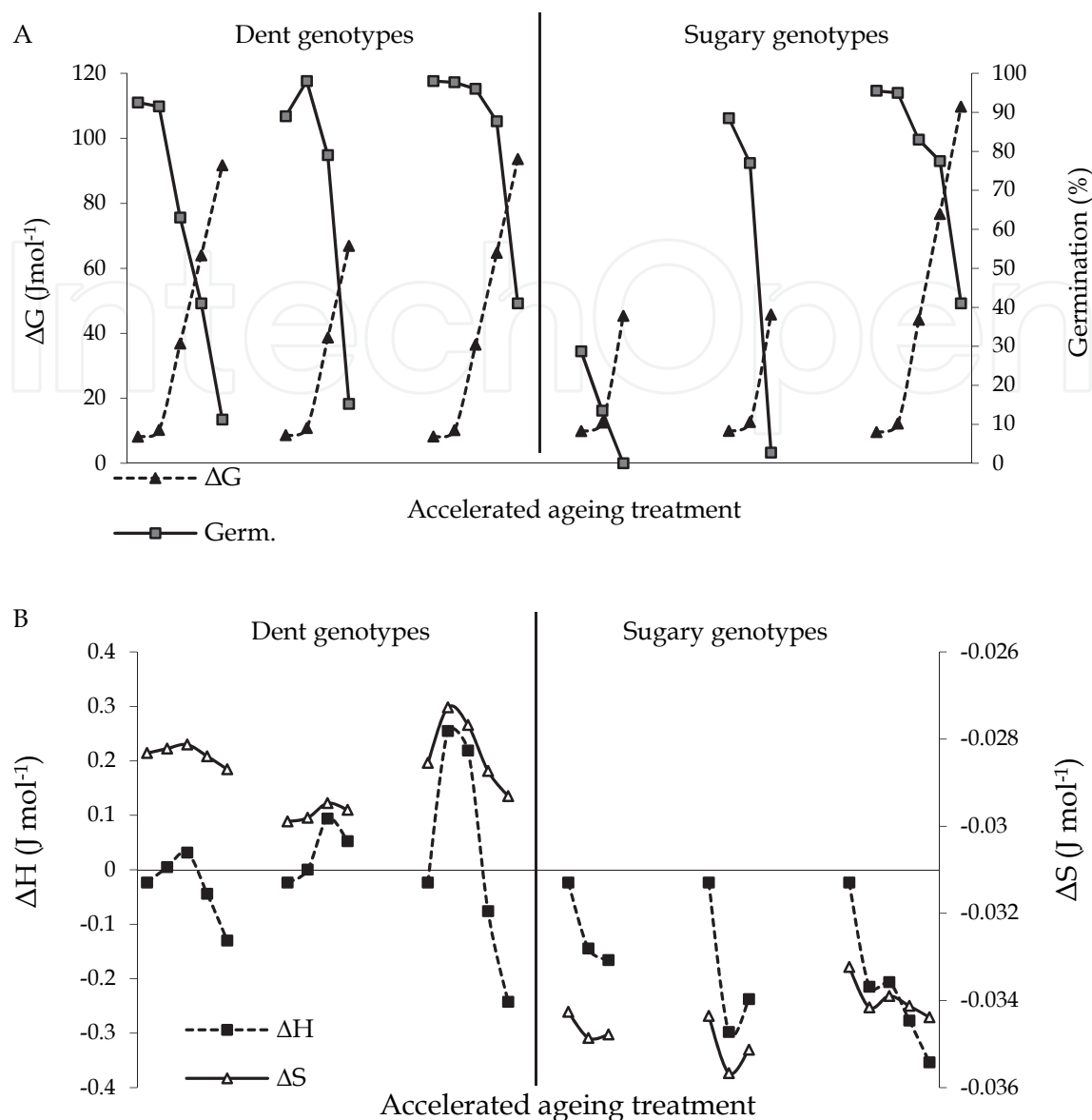


Fig. 2. Differential free energy (ΔG) entropy (ΔS) and enthalpy (ΔH) and decrease in germination of dent maize genotypes and sugary genotypes as functions of time of accelerated ageing

2.2 Importance of redox equilibrium

Life depends on a balance between entropy and enthalpy. For plants, the required energy for maintaining an ordered state is achieved by oxidation (respiration) of photosynthesized substances. Mitochondrial respiration provides energy for biosynthesis and its balance with photosynthesis determines the rate of plant biomass accumulation (Millar et al., 2011). The result of oxidation is an overall reducing environment in cells. During oxidation, photo-oxidative stress and photorespiration, the production of reactive oxygen species (ROS) is an unavoidable consequence (Brosche et al., 2010). ROS production requires or releases some quantities of energy (the voltage of an electrochemical cell is directly related to the change of the Gibbs's energy, Fig. 3), which was briefly described by Vitvitskii (1969) and Buettner (1993):

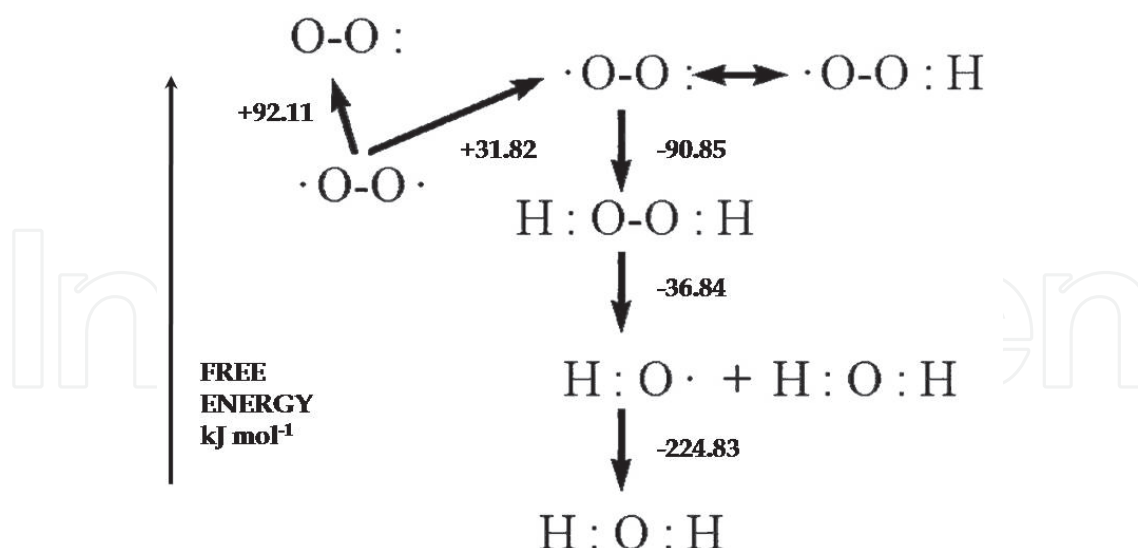


Fig. 3. The free energy of different reactive oxygen species

Redox reactions require redox couples which are responsive to electron flow, which contribute to the distinct reducing/oxidizing environment. Sets of redox couples can be independent from other sets if the activation energies for the reactions are high and there are no enzymatic systems to link them kinetically, which is commonly the case in seeds. Schafer & Buettner (2001) defined the redox environment of a linked set of redox couples, as found in a biological fluid, organelle, cell, or tissue, as the summation of the products of the reduction potential and reducing capacity of the linked redox couples present.

The reduction potential can be described as the voltage (reducing capacity) present in the number of available electrons. The reducing capacity could be estimated by determining the concentration of the reduced species in a redox couple using the Nernst equation:

$$\text{Redox environment} = \sum_{i=1}^n (\text{couple}) E_i [\text{reduced species}]_i \quad (5)$$

where, E_i is the half-cell reduction potential for a given redox pair and (reduced species) is the concentration of the reduced species in that redox pair.

The Nernst equation has a wide range of applications in biology because many biochemical reactions in living organisms involve electron transfer reactions. These reactions are responsible for energy production. The voltage of an electrochemical cell is directly related to the change in the Gibbs energy:

$$\Delta G^0 = -nF\Delta E^0 \quad (6)$$

where n is the number of electrons exchanged in the chemical process, F is the Faraday constant and ΔE^0 is the electromotive force under standard conditions, i.e., the difference in the standard reduction potentials of the two half-cells involved in the process.

Under non-standard conditions, the relationship can be derived from a process such as:



$$\Delta G = \Delta G^0 + RT \ln k \quad (8)$$

$$k = \frac{[\text{Ox}_1]^c [\text{Red}_2]^d}{[\text{Ox}_2]^b [\text{Red}_1]^a} \quad (9)$$

where k is the mass action expression, $RT \ln k$ is a “correction” factor, necessary because of the non-standard conditions.

Using Eq. 5, the voltage of an electrochemical cell can be expressed by the Nernst equation:

$$\Delta E = \Delta E^0 - \frac{RT}{nF} \ln k \quad (10)$$

Understanding the dynamics of the redox elements in biological systems remains a major challenge for redox signalling and oxidative stress research (Schafer & Buettner, 2001). The reduction potential of various redox couples in the cell could be viewed as triggers to activate a cellular switchboard that move the cell through different physiological phases: from proliferation (Fig. 4) through various stages of differentiation and, when stressed or damaged in such a way that the redox environment cannot be maintained, into apoptosis. Necrosis is the complete loss of the ability to activate and/or respond to changes in these nano-switches.

With the exception of stress situations, this phenomenon is connected with planned dismissing of individual parts of an organism, which lose functionality (programmed cell death), such as necrosis of aleurone and seed rest, after shifting to autonomic nutrition (Mrva et al., 2006). This approach represents the first step into a new area of quantitative biology.

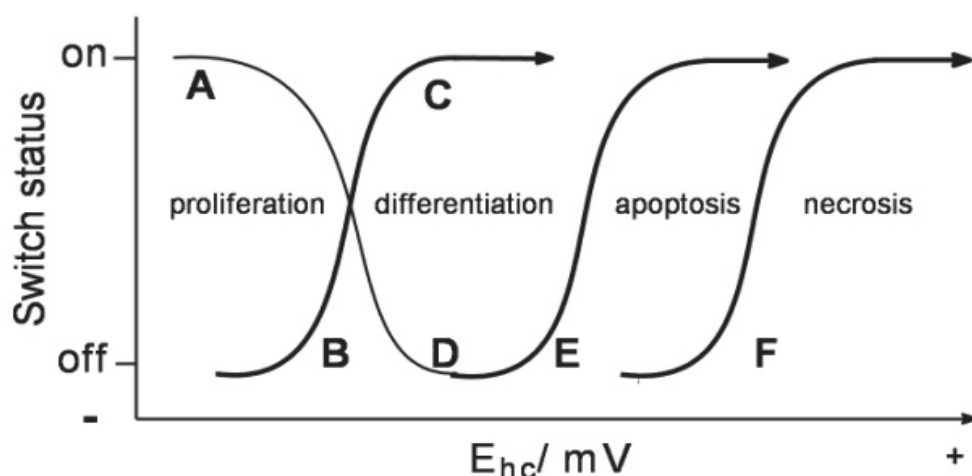


Fig. 4. Reduction potential-driven nano-switches move cells through different biological stages. The redox environment of a cell changes throughout its life cycle. During proliferation the E_{hc} for the GSSG/2GSH couple has its most negative value. (A) The switches for proliferation are fully on. (B) When E_{hc} becomes more positive, the differentiation switches can be turned on while proliferation decreases. (C) The more positive the E_{hc} becomes, the more differentiation switches are turned on until they reach a maximum, when nearly all cells are differentiating. (D) Cells that are not terminally differentiated could undergo proliferation with an appropriate signal and associated redox environment. (E) If the E_{hc} values become too positive, then death signals are activated and apoptosis is initiated. (F) Very high values of E_{hc} , resulting from severe oxidative stress, leave only necrosis as the path to cell death. Data from Schafer & Buettner (2001).

The redox couples and quantification of physiological states are not only important for seeds, but also for all phases of any living system. They contribute to stress tolerance, increase the enthalpy of a system, manage development and, as such, the life cycle on the cellular level. From that point of view plants develop a series of pathways at different levels that combat with environmental stress, which produces more ROS (Shao et al., 2008). These pathways include the photorespiratory pathway, enzymatic and non-enzymatic pathways, corresponding responsive-gene regulation and anatomical ways, which includes drought, salinity, low temperature, UV-B and others.

3. Thermodynamics of germination and plant growth

The introduction of universal thermodynamic parameters could enable a better understanding of the processes of growth and reactions, such as hydrolysis and biosynthesis, incorporated in seed germination. Boyer (1969) quantified water transport into plant based on the energy concept. In addition, the input of water was determined as energy input (Manz et al., 2005; Kikuchi et al., 2006). Recently, Sun (2002) recognized free energy input by water as the presumable factor of plant growth. Moreover, plant growth is also the result of biomass (substance) assimilation and from that point of view Hansen et al. (1998) and Smith et al. (2006) proposed thermodynamic model to describe relation between plant growth and respiration rates (metabolism efficiency). When considered together, simultaneously measured values of CO₂ production rate, O₂ use rate and metabolic heat rate provide a link between cellular and whole-plant processes. 25 KJ mol⁻¹ is taken as total enthalpy change per mole of carbon incorporated into biomass.

3.1 Germination as the double phase shifting of water

During the imbibition, seeds absorb high water quantities during a relative short period, which depend on the species, *i.e.*, the chemical composition of seeds and their condition (Copeland & McDonald, 2001; Boyd & Acker, 2004). The time curve of water absorption has a sigmoid shape (Beardmore et al., 2008; Siddiqui et al., 2008). The rapid entrance of water by the laws of diffusion and osmosis, present during phase I of imbibition (Fig. 1), is followed by enthalpy domination and an increase of the free energy status, present during phase II of imbibition (Sun, 2002). Moreover, imbibition and germination are thermally dependent processes (Sun, 2002; Nascimento, 2003; Taylor, 2004). The energy required for their activation is provided by the temperature of the environment and, in the next step, the energy of the double phase shifting of the water front (Osborne et al., 2002; Volk et al., 2006), which enters through channels under defined temperature conditions (Heimburg, 2010). After water access, the energy necessary for biochemical reactions preceding germination is produced by intensive respiration, activated during the first hours of imbibition (Sanchez-Nieto et al., 2011). The entered and on this way produced energy activates a whole range of reactions, including hydrolysis and biosynthesis (Copeland & McDonald, 2001), as concomitant processes, thereby further increasing the energy, which is required for growth. From this point of view, the free energy can be defined by both: the water volume in the seed/seedling system and the constants of hydrolysis of condensed seed substances and biosynthesis of the plant *de novo*.

Sun (2002) delineated that water sorption is an exothermic event (Fig. 1). A high negative enthalpy value at low water content suggests the strong affinity of water molecules to polar sites. As the water content increases, the enthalpy becomes less negative. As process based

on volume increasing, sorption is temperature dependent category. Moreover, Vertucci & Leopold (1984); Manz et al. (2005); Kikuchi et al. (2006) clarified that the strongest negative enthalpy value occurs at about 7 % water content, and a small negative enthalpy is also observed at moisture contents between 8 % and 25 % (Fig.5). Within this region, the entropy approximates zero. The lack of measurable respiration at moisture contents below 8 % is consistent with the lack of activity for most enzymes at such dry conditions. The region between 8 and 25 % moisture has been termed the region of “restricted metabolism”. This is the range in which liquid water first appears and where the differential entropy values indicate the first solution effects. Within this region of hydration, there are great changes in the ability of the seed to endure excessive and rapid imbibition. The enthalpy is low, but still negative. In the final wetting range, at moisture contents between 24 and 32 %, respiration begins to expand rapidly in response to moisture, when resistance to leakage and chilling injury is established. Damage due to imbibing water is the greatest when the initial seed moisture contents are in the region of strongest water binding. Damage is reduced and finally absent when the seed moisture contents are increased to the second and then to the third level of water affinity. The primary hydration process is considered to be completed when the differential enthalpy of hydration approaches zero. The entropy change reflects the relative order and its peak (Fig. 1 and 5) is presumably associated with the saturation of all primary hydration sites. No consistent differences in the water sorption characteristics has been found between recalcitrant and orthodox seed tissues (Sun, 2000).

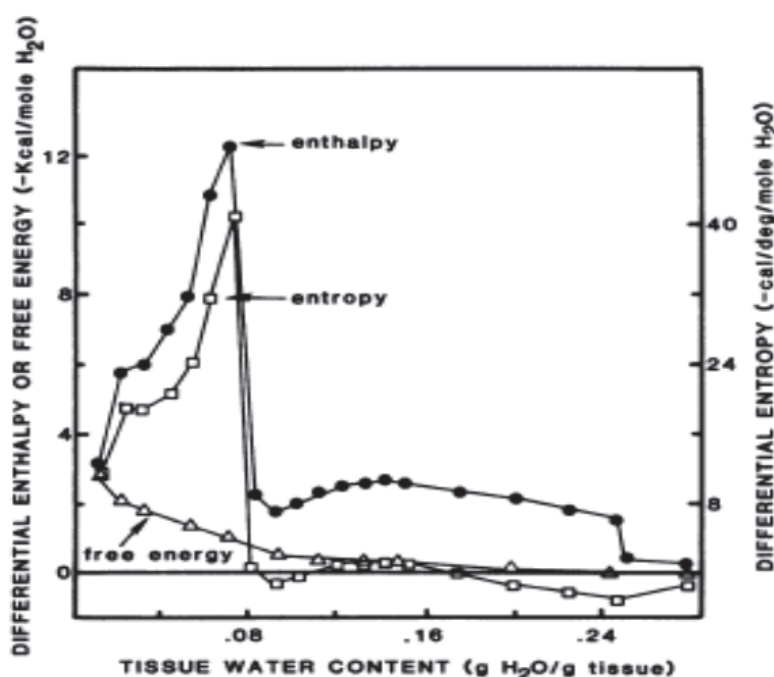


Fig. 5. Differential energies and entropies of water sorption at different moisture contents of ground soybean embryos. Data from Vertucci & Leopold (1984).

Contrary to experimental data realized on viable seeds, Krishnan et al. (2004a, 2004c) established that germinating and non-germinating seeds contained three types of water (bound, bulk and free water) in phase I of hydration. During phase II of hydration, the bulk water of non-germinating seeds disappeared completely, resulting in two types of water. However, three types of water were observed in germinating seeds in phase II. The rapid

hydration in phase III was observed only in germinating seeds. The observed data indicate the importance of free water during the imbibition process, as an activator and bearer of the germination process. The water front brings energy into seed, contributing to an increase in the thermal energy necessary for the commencement of endergonic reactions (activation energy).

3.2 Growth as conversion of energy and substance

When biochemical reactions in imbibed seeds attain a critical point, inducing cell division, germination commences, giving as the product a new plant, resulting from the genome which was stored during shorter or longer periods in the seed (embryo). It is important to underline that one of the most important factors in this moment is triggering of different developmental phases by reduction potential-driven nano-switches. The next phase is characterized by water and substance distribution (allocation) from hydrolysed seed substances, denoted as the plant growth - biosynthesis. Although living systems are non-linear thermodynamic systems, which are far removed from equilibrium (Trepagnier et al., 2004), it is necessary to hypothetically define an energy balance for partial phases and processes. This could be enabled through the introduction of the basic processes of germination: hydrolysis and biosynthesis, as well as the status of their free energy, derived from the reaction constants.

$$\Sigma Hy = DW_{seed} - DW_{seed\ rest} \quad (5)$$

$$\Sigma Bs = DW_{root} + DW_{shoot} \quad (6)$$

$$Cc = \Sigma Hy / \Sigma Bs \quad (7)$$

$$Dev = DW_{seed} - (\Sigma Bs - DW_{seed\ rest}) \quad (8)$$

where ΣHy is the sum of hydrolysis, ΣBs is the sum of biosynthesis, DW is the dry weight of seed, as well as root, shoot and seed rest, as parts of seedling in monocotyledonous plants (in dicotyledonous plants, cotyledons are seed rests and they are photosynthetically active), Cc is coefficient of seed substance conversion, Dev is devastated substance.

$$G_{Wc} = -RT \ln (W_c) \quad (9)$$

$$kHy = \Sigma Hy \times DW_{sed\ rest} / DW_{seed} \quad (10)$$

$$kB_s = \Sigma Bs \times Dev / \Sigma Hy \quad (11)$$

$$G_{Hy, Bs} = -RT \ln (k) \quad (12)$$

where G_{Wc} is the free energy, based on water volume according to the Clausius-Clapeyron equation for the heat of vaporization (Eq. 1), G_{Hy} is the free energy of hydrolysis and G_{Bs} is the free energy of biosynthesis, based on the reaction constants, R is the gas constant and T is the germination temperature, rendered as the sum of the average daily temperatures.

After the imbibition, the initial growth (germination process) is followed by substance conversion: from the hydrolysed seed substance into biosynthesised substance of the root and shoot, since the young plant is not capable to produce its own substance by photosynthesis (chlorophyll has not been synthesised or its quantity is under a critical

amount). Regarding the fact that the seedling's parts grow unequally (Vysotskaya, 2005; Rauf et al., 2007), which is a particular characteristic of the starting phases of germination, so as their free energy is unequally distributed. Experiments on seed ageing (Dragicevic et al., 2007, Dragicevic, 2007) demonstrated that the highest energy potential of 7-day old seedlings was present on the shoot level, then on the seed rest level and finally on the root level. In comparison to energy introduced by the hydration process, the free energy of hydrolysis and particularly of biosynthesis had significantly lower absolute values. Moreover, the consequences of deterioration processes on the seed/seedling level are present in the absorption of high water quantities and it was defined as "water induced growth" by Boyer (1969), which is a negative state for the system. Contrary to the high energy status introduced into the seed/seedling system by water, the free energy of hydrolysis tends to have minimal variations, while the free energy of biosynthesis had values closest to equilibrium, tending upon higher order of biosynthetic reactions. It is important to emphasise that the domination of exergonic reactions (Davies, 1961; Sun, 2002) is important for the release of the necessary energy and the more intensive they are, the greater is the growth potential of the system. According to the Hess Law, free energy is cumulative, irrespective of its origin; hence, all the potential energy present in a plant system is given by the sum of the individual energy states, resulting from the double phase shifting of water and that released from all the hydrolysis and biosynthesis reactions.

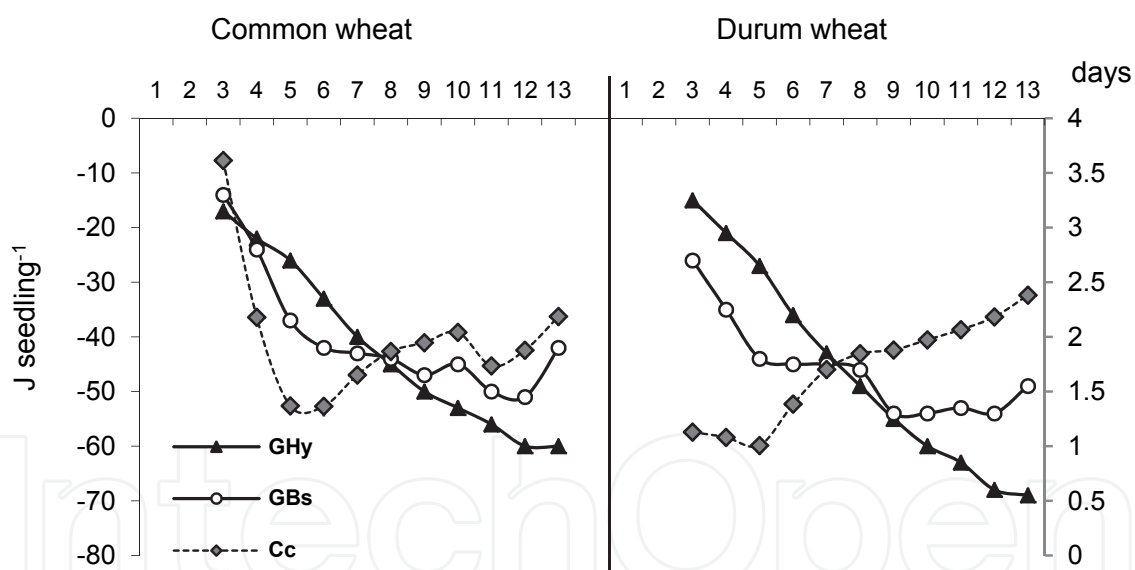


Fig. 6. Dynamics of the coefficient of conversion (C_c) of the free energy of hydrolysis (G_{Hy}) and biosynthesis (G_{Bs}) during 13 days of germination

After germination, the growth process is followed by less or more intensive water absorption, as well as substance synthesis. Experiments with wheat (Dragicevic et al., 2008) showed that the free energy of hydrolysis increased linearly (Fig. 6), while the free energy of biosynthesis fluctuated, with the coefficient of conversion. The observed non-linearity could indicate a change in the balance between exergonic and endergonic reactions. Moreover, the inputted and released energies are the result of process and reactions which minimize the energies of a given system. In living, as highly hydrated systems, energy is inputted by water and the total energy of the reactions has to be in a stable equilibrium.

The important points of germination and growth processes are substance losses, which Tukey (1970) defined as devastated substance. This substance includes losses through respiration (Kuziyakov & Larionova, 2005; Hill et al., 2007), as well as exudates of roots (Tukey, 1970; Jones et al., 2009) and it is calculated as illustrated in Eq. 8. The leaching (devastation) of hydrolysed substance from a seed-seedling system also means the permanent lost of energy and it starts with imbibition. Sredojevic et al. (2008) established that for soybean about 36 % and for sunflower about 46 % of free energy was lost between the 1st and 8th, i.e., 10th day, of the germination process by the leaching process alone.

The rate of plant growth is proportional to the product of the metabolic rate and the metabolic efficiency for the production of anabolic products. Over much of the growth temperature range, the metabolic rate is proportional to the mean temperature and the efficiency is proportional to the reciprocal temperature variability (Criddle et al., 2005), what could be considered as improvement in understanding of energy and biomass conversions, according to previous model purposed by Hansen et al. (1998) and Smith et al. (2006).

3.3 Growth as a flow process

In living systems, the largest flow of water is from soil, through plants to the atmosphere, the so-called by Yeo & Flowers (2007) soil-plant-atmosphere continuum. The driving force for this water continuum is the difference in free energy between liquid water in the soil and water vapour in the atmosphere. The driving forces diverge upon the different parts of the system. Water movement in soil depends on depth of the soil profile and on the forces that bind water in the capillaries (between soil particles). Water can move in plants through a matrix composed of capillaries (the cell walls) or by tubes (the xylem and phloem) where bulk flow of water occurs under pressure gradients. Water movement between cells depends on the properties of the membranes, which are differentially permeable.

In plants, water moves passively by the potential gradient of water (through semi-permeable membranes) or the potential gradient of pressure (without semi-permeable membranes). Solutes moving across semi-permeable membranes due to the potential gradients of water, combining both: the solute potential and the hydrostatic pressure, with decreasing of free energy of water.

Plants can change intracellular solute potentials, thereby influencing water flow. Water can move in a plant against its water potential only when coupled to the movement of solutes, decreasing the free energy of the solute and when the general net change of free energy (solute and water) is negative. Flow across membranes is passive in response to differences in the water potential and occurs primarily through aquaporins (integral membrane proteins) rather than directly through an impermeable membrane. Aquaporins can be gated reversibly, so that plants may be able to control their plasma membrane water permeability. Transportation of an uncharged solute uphill against its concentration gradient (Taiz & Zeiger, 2010) from lower to higher concentrations decreases entropy and requires the input of free energy:

$$\Delta G = 2.3RT \log ((C_2)/(C_1)) \quad (13)$$

If $C_2 > C_1$, then $\Delta G > 0$ and work is required to make this transfer. However, movement such as by diffusion can proceed spontaneously from C_2 to C_1 when $C_2 > C_1$, since this increases entropy and $\Delta G < 0$.

The change in free energy when moving one mole of a substance or ion against the membrane potential when considering the work required or performed arises from both the voltage (“electro”) and concentration (“chemical”) gradients.

Ions tend to flow from areas of higher to lower electrochemical potential so that ΔG is negative, which defines the maximal work output a reaction can perform. Cellular functions are ultimately linked to metabolic fluxes brought about by thousands of chemical reactions and transport processes.

The direction of flux is dictated by the change of Gibbs free energy which can be expressed through the thermodynamic equilibrium constant K_j^{equ} as follows (Holzhutter, 2004):

$$\Delta G_j^{(0)} = -RT \ln(K_j^{\text{equ}}) \quad (14)$$

where $\Delta G_j^{(0)} \leq 0$ is the change of free energy under the condition that all reactants are present at unit concentrations, $K_j^{\text{equ}} \geq 1$.

With accumulating concentrations of the reaction products (appearing in the nominator) and/or vanishing concentrations of the reaction substrates (appearing in the denominator) (Eq. 13), the concentration-dependent term (Eq. 14) may assume negative values, i.e., in principle, the direction of a chemical reaction can always be reverse provided that other reactions in the system are capable of accomplishing the required change in the concentration of the reactants. From this point of view, the introduction of irreversible thermodynamics (Yeo & Flowers, 2007) imposes upon research of biological fluxes, as more general view, which includes various forces. It applies the parameters used in classical thermodynamics to non-equilibrium conditions, i.e. in situations where there is the net flux of a substance, although the system must be close to equilibrium.

4. Conclusion

Plants are non-linear systems determined by inheritance and dependent on temperature and time, they exist owing to the opposing metabolic processes:

1. Those which consume energy and produce substances (photosynthesis);
2. Those which utilize substances and release stored energy to increase enthalpy, as well as to maintain their own status close to a steady state, which increases entropy.

Every plant attempts to maintain structure with the minimal expenditure of energy: they are able to conserve energy in substances; hence they form structures with stored energy to surpass negative conditions and to increase their reproduction ability. The consequence is the formation of seeds in higher plants.

A seed is a biological system in a vitrified state. Regardless of the fact that vitrification presents conservation state for seed systems (close to a steady state), silent metabolic processes, with lower abilities to counter developed injuries, are present. This means that vitrification has a double nature: conservation (low entropy and enthalpy) with low ability of recovery. Long storage could induce deterioration, which is related to changes in the internal energy of the system. In general, the values of the critical limits of the thermodynamic parameters decrease with increasing temperature. The differential enthalpy and entropy increase in seeds with storage time and became asymptotic as the seeds lose their viability. A radical drop in germination follows the trend of ΔG increase and ΔH

decrease (with values $< 0 \text{ J mol}^{-1}$), indicating intensification of endergonic reactions, as well as a parallel shift of the system from a relatively ordered to a random state.

One of the important factors present during any deterioration or stress is electron transfer, inducing the production of free radicals, which are responsible for energy production. A reduction of the potential of various redox couples in a cell could be viewed as a trigger to activate cellular switchboards that move the cell from proliferation through various physiological stages into apoptosis and finally, necrosis (equilibrium). The redox couples are important for all living systems, vitrified or hydrated: they contribute to stress tolerance, and manage development and by this, the life cycle on a cellular level.

The germination process requires energy, which is provided by the environmental temperature and, in the next step, by the energy of the double phase shifting of the water front, under defined temperature conditions. The entered and in this way produced energy activates a whole range of reactions, including hydrolysis and biosynthesis, as concomitant processes, increasing, as a consequence, also the energy. When the biochemical reactions in imbibed seeds reach a critical point, inducing cell division, germination commences, giving as a product a new plant. The next phase is characterized by the distribution of water and substances (from hydrolysed seed substance), denoted as the plant growth - biosynthesis. In comparison to the energy introduced by hydration processes, the free energy of hydrolysis and, particularly, of biosynthesis have significantly lower absolute values. The domination of exergonic reactions is the release of the necessary energy and the more intensive they are, the higher is the growth potential of the system.

From that point of view, water with its characteristics, redox signals and substance conversion (including environment) are crucial points of processes providing in plants, they are dependent on energy flow and its transformations in plant systems.

Furthermore, plant growth is provided for by water flow and substance accumulation. The driving force for soil-plant-atmosphere water continuum is the difference in free energy between liquid water in the soil and water vapour in the atmosphere. Cellular functions are ultimately linked to metabolic fluxes which direction is dictated by the change of the free energy, too.

The introduction of universal thermodynamic parameters, as well as irreversible thermodynamics could lead to a better understanding of the growth process and consecutive reactions such as hydrolysis and biosynthesis, as parts of seed germination. The free energy input by water is a presumable factor of plant growth. From this point of view, free energy can be defined by the water volume in seedling/plant, as well as the constants of substance conversion. Namely, energy generation in seedling arises from the double phase shifting of the absorbed water and by its liberation *via* hydrolyses and biosyntheses. Consequently, a combined approach of thermodynamics and biochemistry could be established as a method for quantification of physiological processes, with an ecological background in the selection and breeding of new genotypes in crop production.

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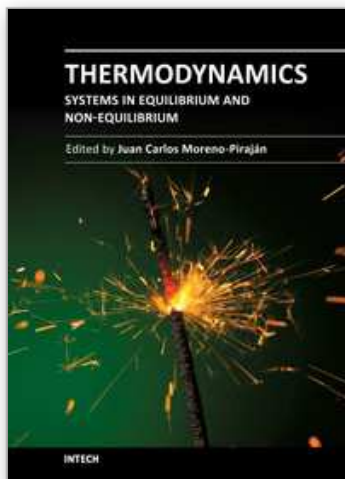
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