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PAAVO PELKONEN

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TEMPERATURE RESPONSE OF  
ELECTRICAL IMPEDANCE IN  
POPLAR CUTTINGS:  
A PRELIMINARY CONCEPT

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POPPELIPISTOKKAIDEN  
IMPEDANSSIN RIIPPUVUUS  
LÄMPÖTILASTA:  
ALUSTAVA MALLI

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Metsäntutkimuslaitos on maa- ja metsätalousministeriön alainen vuonna 1917 perustettu valtion tutkimuslaitos. Sen päätehtävänä on Suomen metsätaloutta sekä metsävarojen ja metsien tarkoituksenmukaista käyttöä edistävä tutkimus. Metsäntutkimustyötä tehdään lähes 800 hengen voimin yhdeksällä tutkimusosastolla ja yhdeksällä tutkimus- ja koeasemalla. Tutkimus- ja koetoimintaa varten laitoksella on hallinnassaan valtion-metsiä yhteensä n. 150 000 hehtaaria, jotka on jaettu 17 kokeilualueeseen ja joihin sisältyy kaksi kansallista ja viisi luonnonpuistoa. Kenttäkokeita on käynnissä maan kaikissa osissa.

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Paavo Pelkonen

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Poppelipistokkaiden impedanssin riippuvuus  
lämpötilasta: Alustava malli

*Approved on 12.10.1984*

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The response of electrical impedance to changes in the long-term ambient temperature 3—4 days before, and to changes in short-term artificial night frosts were studied using a hypothetical electrical circuitry as a basis for modelling.

The analysis was based on impedance measurements conducted on different poplar clones in the Ontario Tree Improvement and Forest Biomass Institute, Ontario, Canada in 1982.

The agreement between the changes in the observed and calculated electrical impedance was good. The effective time to the prevailing temperatures was four days according to the results of the present study. The conditioning to the long-term ambient temperature had an effect on the changes in the electrical impedance caused by the night frosts.

Even if the model, presented in this report, involves several assumptions, it does provide a basis for further data analysis and synthesis. The model makes it possible to distinguish, operationally, the impedance as well as the frost hardiness properties of poplars and other fast-growing tree species.

Tutkimuksessa analysoitiin poppelikloonien runkosolukoiden impedanssimuutoksien riippuvuutta mittausta edeltävien päivien lämpötiloista sekä edeltävän yön minimilämpötilasta. Yöpakkasia simuloitiin kylmalaitteella laboratoriossa. Analysoinnin lähtökohtana oli solukon sähköfysiologisia ominaisuuksia kuvaava analogiamalli.

Mallilla voitiin kuvata luonnossa havaitut impedanssimuutokset tyydyttävästi. Mallin dynaamiset ominaisuudet olivat samankaltaisia solukon ominaisuuksia ilmentävien impedanssimuutosten kanssa. Mittausta edeltävän yön lämpötilan vaikutukset runkosolukon impedanssiin riippuivat selvästi myös mittausta edeltävien päivien lämpötiloista. Akklimoitumista lämpötilaan ja pakkaskestävyyteen selittivät parhaiten neljän mittausta edeltävän päivän lämpötilat.

Tutkimuksessa käytetty malli sisältää lukuisia oletuksia, mutta luo edellytykset menetelmän kehittämiseen ja impedanssimittauksista saatujen aineistojen analyysiin ja synteisiin. Tarkan ja luotettavan mallin avulla on mahdollista tutkia poppeleiden samoin kuin muidenkin nopeakasvuisten puulajien impedanssiominaisuuksia ja talvenkestävyyttä.



# 1. INTRODUCTION

The prevailing long-term mean temperature has a clear influence on the ability of forest trees to withstand low temperatures, and also affect postfreezing impedance characteristics (Van den Driesshe 1973, Timmis 1976). A similar effect of preconditioning temperatures has been noticed in studies on other physiological processes, like photosynthesis or respiration (Rook 1969, Pelkonen 1980). In general, hardy plants adapt their metabolism to low temperatures and synthesize substances that protect their tissues from various forms of freezing stress (Olien 1978).

According to Glerum and Krenciglowa (1970), the tissue circuit of trees consists of a complex combination of resistors and leaky capacitors which are connected in series and in parallel, but predominantly parallel. Since each type of tissue has its own impedance characteristics, it is difficult to gain an

understanding of the physiological changes in trees on the basis of impedance measurements (Glerum and Krenciglowa 1970).

Electrical network models have been proposed for describing the electrical system in tissues and to determine the impedance, but questions still remain which prevent the wider utilization of the method. Study materials with a similar distribution of periderm, phloem, cambium and xylem provide, however, a suitable basis for investigating the response of impedance characteristics to a changing environment.

The aim of the present study was to investigate the response of electrical impedance to changes in the long-term ambient temperature 3—4 days before, and to changes in short-term artificial night frosts. A hypothetical electrical circuitry was used as a basis for modelling.

# 2. MATERIAL AND METHOD

The analysis was based on impedance measurements conducted on eight different poplar clones. Fifteen cuttings of different clones were sampled in the field once a week from October 5 to November 23, 1981. The last round of sampling was performed in the winter on January 18, 1982. After being transferred to the laboratory, the cuttings were subjected to three over-night freezing test temperatures. The temperatures varied from  $-6$  to  $-40^{\circ}\text{C}$ , being higher at the beginning and lower at the end of the test period (Oct. 5, 1981 — Jan. 18, 1982). Five cuttings from each clone were placed in plastic bags and then put into the freezing unit for testing at different temperatures.

Thermocouples were inserted into the plastic bags and cuttings in order to monitor the temperatures during freezing. The maximum change (per hour) at temperatures below  $0^{\circ}\text{C}$  varied depending on the minimum temperature, from  $2$  to  $6^{\circ}\text{C}$  during the freezing test. The cuttings were removed from the freezing unit after thawing. The cuttings were kept in cold storage at  $+4^{\circ}\text{C}$  before and after freezing and for about 1 hour at room temperature in the laboratory prior to carrying out the measurements.

The clones and measurements are described in detail in an earlier report (Pelkonen 1984). The calculations presented here are for the least frost hardy clone (DN 22) and for the hardest clone (TAC 8).

The following assumptions, based on evidence from the literature, were made for the analysis.

1. There is a concentration gradient in undamaged tissue caused by the influx of ions from the extracellular solution (Palta and Li 1978).
2. An enhanced passive efflux of ions takes place due to freezing damage (Palta and Li 1978).
3. The conductivity of the intracellular and extracellular solutions is influenced by electrolytes, mainly  $\text{K}^+$  ions (Palta and Li 1978).
4. The efflux of ions increases the intracellular and decreases the extracellular resistance and vice versa.
5. There is interaction between the preceding temperature conditions and the amount of damage resulting from freezing (Van den Driesshe 1978).
6. In freezing kinetics, the factor that affects the equilibrium pattern of phase transition, which occurs as a function of temperature, has to be differentiated from the factor that affects displacement from equilibrium, which occurs as a function of the rate of temperature change (Olien 1978).

### 3. RESULTS

The electrical 1 kHz and 1 MHz impedance applied to the different clones fluctuated before and after the freezing treatments during the test period (Oct. 5/81 to Jan. 18/82). Although there were clear genetic differences between the clones, certain similarities were observed in their response to temperature.

The physiological processes of the tree are adjusted so as to best suit the prevailing environment. Thus it is a one-way relationship of a dependent variable (physiological processes) responding to an independent variable temperature. The late-fall electrical impedance is characterized by two factors, one of which varies dramatically with the low night temperatures, the other gradually increases with the progression of dormancy.

A simple approximation for the effective long-term temperature ( $T_s$ ) was made on the basis of the minimum temperatures ( $T_n$ ) and the daily mean temperatures ( $T_m$ ) of four preceding days (i) in the field. Then:

$$(1) \quad T_s = (\sum_{i=1}^4 T_{ni} + \sum_{i=1}^4 T_{mi})/4.$$

In order to quantify post-freezing electrical impedance two factors were assumed to affect its change. i) The effect of the change in temperature ( $E_c$ ). Then:

$$(2) \quad E = a(T_s - T_k)^2 + 1$$

where (a) reflects the sensitivity of various clones to changes in temperature.  $T_k$  is the minimum temperature during the temperature treatment.

ii) The effect of freezing temperature ( $E_f$ ). Then:

$$(3) \quad E_f = b^{-T_k}$$

where (b) reflects the physical constant of ice crystal formation.

It has been assumed that the effect of the change in temperature and of freezing is multiplicative. Thus, the total driving force due to temperature ( $E_t$ ) that causes the change in the electrical impedance can be calculated as:

$$(4) \quad E_t = E_c \cdot E_f$$

Furthermore, there is a one-way relationship between the intracellular electrical resistance ( $R_1$ ) and the total driving force due to temperature ( $E_t$ ). The intracellular resistance was calculated according to the following formula:

$$(5) \quad R_1 = r_2 \cdot (E_t + r_1) / (r_2 + E_t + r_1)$$

where ( $r_1$ ) is the minimum and ( $r_2$ ) the maximum value of the intracellular resistance.

The extracellular resistance ( $R_2$ ) is related to the intracellular resistance ( $R_1$ ) due to the ion flux and was calculated as follows:

$$(6) \quad R_2 = r_2 - R_1.$$

The capacitive reactance ( $X$ ) of the cellular membrane is associated with the driving forces of the electrolyte flux and was quantified using the following equation:

$$(7) \quad X = r_2 + r_1 \cdot (1 + E_t \cdot E_f).$$

The impedance of an electrical network of tissue involves intracellular resistance ( $R_1$ ), the extracellular resistance ( $R_2$ ) and, the membrane capacitance ( $X$ ). For 1 kHz and 1 MHz it is given by the simplified formulae:

$$(8) \quad Z_{\text{kHz}} \approx \sqrt{R_1^2 + X^2} \cdot R_2 / \sqrt{R_1^2 + X^2} + R_2$$

$$(9) \quad Z_{\text{MHz}} \approx R_1 \cdot R_2 / (R_1 + R_2)$$

In order to compare the variation between measured and calculated values for clones DN22 and TAC8, the maximum relative intracellular resistance ( $r_2$ ) was assumed to be 100 for both clones (Eqs. 5 and 7) (Figs. 1—2). There was moderate agreement between the variation in the calculated and measured values when parameter (b) (Eq. 3) was 1.07 for both clones,  $r_1$  was 25 for DN22 and 38 for TAC8 and parameter (a) (Eq. 2) was 0.05 for DN22 and 0.015 for TAC8. The great difference between minimum ( $r_1$ ) and maximum ( $r_2$ ) intracellular resistance was generally indicated by a high 1 kHz/1 MHz ratio for the frost sensitive clone. The low value of 0.015 for parameter (a) in TAC8 (in



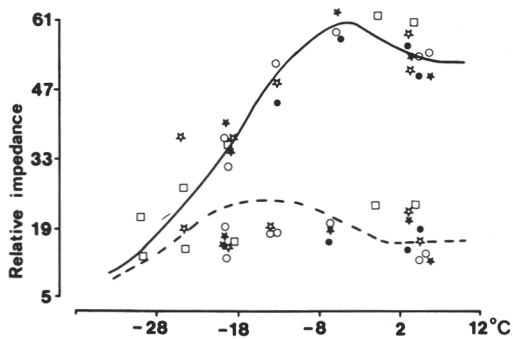


Figure 1a. The calculated 1 kHz (—) and 1 MHz (---) impedance values, plotted against the night temperature preceding measurement. The prevailing temperature ( $T_s$ ), used for the calculations, was  $+8^\circ\text{C}$ . The respective measured values of clone DN22 are presented on the basis of weekly measurements according to the following symbols:  $\circ$  = 1st,  $\bullet$  = 2nd,  $*$  = 3rd,  $\star$  = 5th,  $\square$  = 6th week.

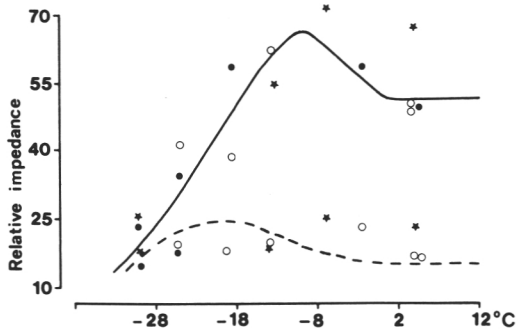


Figure 1b. As Fig. 1a, but the prevailing temperature ( $T_s$ ) used for the calculation was  $+1^\circ\text{C}$  and for the following weeks:  $\circ$  = 4th,  $\bullet$  = 7th,  $*$  = 8th.

DN22;  $a=0.05$ ) indicated a high stability to changing temperatures.

Owing to the difference between the maximum true intracellular resistance and the maximum relative intracellular resistance ( $r_2$ ) used in the calculations, the magnitude of the calculated 1 kHz impedance was 2.3 times higher than the measured impedance. The curves presented in Figs. 1—2 were corrected

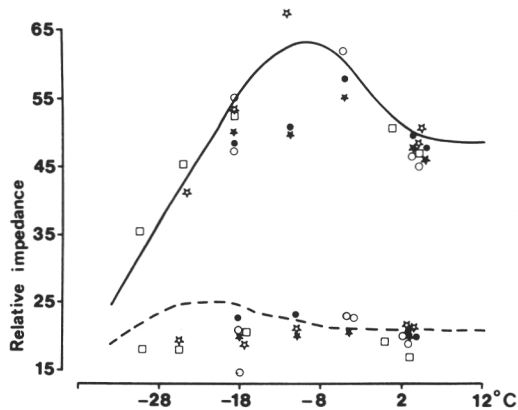


Figure 2a. As Fig. 1a, but for the clone TAC8.

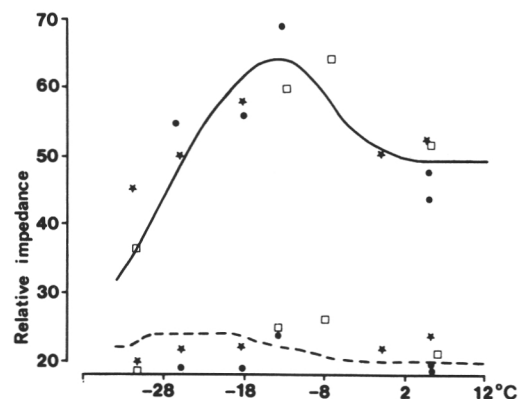


Figure 2b. As Fig. 2a, but the prevailing temperature ( $T_s$ ), used for the calculations, was  $+1^\circ\text{C}$  and for the following weeks:  $\circ$  = 4th,  $*$  = 7th,  $\square$  = 8th.

for this difference. The agreement between measurements made at 1 MHz and the calculated values was poor. The measured impedance values varied more as a result of freezing than was expected on the basis of the model. The magnitude of the calculated impedance at 1 MHz was 2.6 times higher than the magnitude of the actual measurement.

## 4. DISCUSSION

For calculations with the model two different features in the temperature response of impedance were separated: 1) The response to prevailing temperatures on preceding days and 2) the response to minimum temperatures on preceding nights. On the basis of these temperature responses two driving forces were calculated in association with the impedance changes: 1) The effect of freezing temperature and 2) the effect of the rate of temperature change. The effects of interaction between different types of temperature responses has been found for different kinds of plants in frost hardiness studies (Van den Driesshe 1973, Olien 1978).

The effective time interval for the response to the prevailing temperature was four days according to the results of the present study. Only daily minimum, maximum and mean temperatures were available and more frequent data can result in another time interval. For instance, the temperature preceding the 8th measurements dropped fast over a period of several days and the physiological stage of development of the poplars was perhaps not able to adapt rapidly enough to changes in temperature (Pelkonen 1984). The impedance measurements clearly indicated that the effective prevailing temperature, with respect to the internal state of the cuttings, was higher in the 8th week than was expected on the basis of the temperatures for the temperatures for the four preceding days. However,

the time interval in the temperature response for poplars seemed to be clearly shorter than the respective interval for conifers found in earlier studies (Timmis 1976).

There may be several reasons for the poor agreement between the variations in measured and calculated 1 MHz impedance values. First of all, the model is most probably too simple to describe impedance properties in tissues. For instance, the cell wall resistance has not been taken into account. The effect of cell wall resistance in series with intracellular resistance is more pronounced at 1 MHz than at 1 KHz, and it shifts the maximum values of impedance response curve towards the high temperatures, which is to be expected on the basis of measurements. In addition, the measurements at 1 MHz involve numerous technical problems which may also affect the final results. The effect of cell wall resistance, however, could be easily tested, but the most important task in developing this technique is the analysis of the properties of the individual components in the complex system.

Even if the model, presented in this report, involves several assumptions, it does provide a basis for further data analysis and synthesis. The reliable model makes it possible to distinguish operationally, the impedance as well as the frost hardiness properties of different poplar clones.



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*Total of 8 references*

## SELOSTE

### **Poppelipistokkaiden impedanssin riippuvuus lämpötilasta: Alustava malli**

Solukoiden sähköfysiologisiin ominaisuuksiin perustuvan mallin avulla tutkittiin lämpötilan vaikutuksia poppelin pistokkaiden impedanssiin (vaihtovirran vastus). Laboratoriomittaukset, joihin analysointi perustuu, tehtiin Kanadassa, Ontariossa, Ontario Tree Improvement and Forest Biomass Institute:ssa syksyllä ja talvella 1981—1982. Laboratoriomittauksissa koottiin aineistoa kahdeksasta poppelikloonista, mutta tässä työssä esitettyyn tarkasteluun valittiin kaksi kloonista, joista hybridikloonin DN 22 pakkaskestävyys oli melko heikko ja pohjois-ontariolaista alkuperää olevan kloonin TAC 8 pakkaskestävyys oli hyvä.

Analogiamalli perustui olettamukseen, että solunsisäinen resistanssi on kytketty sarjaan solumembraanin kapasitiivisen reaktanssin kanssa ja niiden kanssa rinnan on kytkettynä soluvälin resistanssi. Edelleen on oletettu, että membraanin yli vallitsee vaurioitumattomassa solukossa ionien konsentraatiogradientti, joka solujen vaurioitumisen seurauksena pienenee membraanien läpäi-

sevyysominaisuuksien muuttuessa. Analysoinnissa käytetyn mallin avulla pystyttiin kuvaamaan lämpötilan vaikutus solukoiden ominaisuuksissa tapahtuviin muutoksiin. Lämpötilavaikutuksessa erotettiin pitkäaikainen vaikutus, jota tarkasteltiin mittauksia edeltävien neljän päivän lämpötilojen keskiarvona sekä nopea lämpötilavaikutus, jonka aiheutti mittausta edeltävän yön minimilämpötila. Puiden akklimoituminen lämpötilaan havaittiin laboratoriossa simuloitujen yöpakkasten aiheuttamina muutoksina solukkojen impedanssissa.

Tutkimuksessa käytetty malli sisältää lukuisia olettamuksia, mutta sen avulla voidaan tutkia ja kehittää impedanssimenetelmää, niin että sillä mitattavat tunnuksat kuvaavat mahdollisimman hyvin puiden kestävyysominaisuuksia. Luotettavan mallin avulla eri kloonien talvenkestävyysominaisuuksien tarkastelu on mahdollista elävää materiaalista melko vähäisillä laboratorionkeilla.





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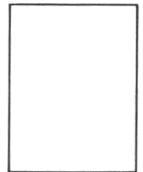
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