Plant electrophysiological reactions to specific environmental conditions

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Abstract
Plant cells exhibit as much electrical activity as aninmal cells but the nature of these electrical variations is not always well understood, especially at the organism level. Damaging a plant, transitions from darkness to light and back, mechanical shocks, temperature shocks and pathogen attacks have been shown to elecit changes in plant electrical patterns at the organism level under laboratory conditions, but plant electrical behavior in the wild is comparatively less well studied. Here we show that by using simple extracellular voltage measurements across a number of wild plant species it is possible to identify associations between very specific environmental conditions and patterns of electrical variation on the scale of seconds to hours in the plants exposed to them. This work has potential applications in using plants as environmental sensors.

Keywords: Plant electrophysiology, environmental conditions, independent component analysis, discrete fourier transform, plants as sensors, vapor pressure deficit

Introduction
Electrical signals in plants have been under investigation since their discovery in the 19th century. The study of plant electrophysiology has advanced in recent decades due to the application of biomolecular and machine learning techniques. Research has shifted from a focus on establishing the conditions for and the consequences of a specific plant electrical signal type that closely resembles the spiking of animal neurons [Trebacz 1998; Koselski 2008; Opritov 2005; Pikulenko 2005; Sukhov 2009/2011] and has taken a broader view by aiming to understand the full variety of fast and slow-onset plant electrical signal patterns [de Toledo 2019] in the context of other known signalling mechanisms [Szechyńska-Hebda 2017; Huber 2019; Yudina 2023], such as molecular transport, volatile organic compound diffusion, mechanical substrate wave [Mancuso 1999; Tran 2019] and acoustic wave propagation [Khait 2018] as well as electrical plant-to-plant signalling [Szechyńska-Hebda 2022]. In this study we aim to answer the question if plant internal state changes in reaction to specific environmental conditions can be identified and characterized by extracellular voltage measurements on plant stems.

Materials and Methods
Six plant species and one control were recorded over periods ranging from 18 to 36 weeks (Table M1), three angiosperm species (Birch, Olive, Magnolia) and three gymnosperm species (Spruce, Larch, Yew) were used. In addition environmental temperature, relative humidity and air pressure were recorded at each plant's location.

1 - Plant species:
Spruce (Picea abies), wild, 10-15 years old, gymnosperm
Larch (Larix decidua), wild, 5-10 years old, gymnosperm
Yew (Taxus baccata), potted outdoor, 3-5 years old, gymnosperm
Birch (Betula pendula), wild, 5-10 years old, angiosperm
Olive (Olea europea), potted outdoor, 5-10 years old, angiosperm

Magnolia (Magnolia soulangeana), potted outdoor, 2-5 years old, angiosperm

2 - Location and climatic conditions:
All plants were located in the austrian Alps at altitudes between 800 and 1000 meters, within an area of approximately one square Kilometer. The wild plants at 1000 m altitude on a sunny, southward-facing side of a valley in the Lungau region, the potted plants at an altitude of 800 m. A brief description of the climatic conditions (all values yearly averages): Hottest month July (18 C), coldest month January (-1 C), wettest month September (137mm), driest month January (39mm), annual precipitation 1012mm, average relative humidity 76%, average pressure 1017 mbar.

3 - Voltage measurement equipment and recording setup:
The electrophysiological recording equipment consisted of one stainless steele needle electrode (E1) horizontally inserted into each plant's stem at the height of the canopy, between approximately 40 cm and 2 m above ground depending on plant size, a second identical electrode (E2) inserted into a branch at the same height as the first electrode as well as a third reference electrode (E0) either inserted into the lower portion of the plant stem just above the ground or directly into the ground substrate. The two highest placed electrodes on each plant were connected to the inputs of a high impedance, two-channel DC voltage amplifier (gain: 2-3) while the third electrode (E0) was connected to the amplifier's reference input. This way the voltage difference between each stem/branch electrode and the reference electrode was measured for every plant continuously over a period ranging from 18 weeks to 36 weeks depending on the plant (Table M1). In addition a control system was created and measured for a period of 10 consecutive weeks. It consisted of a dead piece of branch of 2 cm in diameter and 50 cm in length that had been cut from a P. imperialis tree two years prior, inserted into a pot with garden soil.

4 - Data acquisition and pre-processing:

4.1 - Environmental data
Every plant/control recording location was equipped with a battery powered environmental recorder separate from the battery-powered electrophysiology recorder to avoid electrical crosstalk. Using a BM680 sensor connected to a microcontroller this device measured air temperature (Celsius), relative humidity (%) and air pressure (mbar), writing values to a microSD card once every 31 seconds.

4.2 - Plant and control electrophysiology data
On all plants and on the control system voltages were recorded from electrodes E1 and E2 at a sampling rate of 400 samples per second (sps) on two channels. Timestamped voltage values in the range between -500mV and +1000mV were written to a microSD card by each recording device using a STM32 microcontroller connected to the amplifier. Individual recording sessions lasted between 4 and 7 days with gaps of no more than 30 minutes between sessions in most cases. All recording devices were battery powered to enable power grid independent field operation and to reduce electrical noise to a minimum. To facilitate analysis all recorded voltage data was subsequently resampled to a final rate of 0.25 sps corresponding to one sample every four seconds.

5 - Data processing:

5.1 - Processing environmental data

The raw environmental data timeseries for each plant/control had three dimensions (Temperature, Humidity, Pressure) and one datapoint every 31 seconds. The 20%, 40%, 60%, 80% quantiles for each dimension were calculated using the entire length of the timeseries and used for discretizing each dimension into five equally sized bins labeled 'verylow', 'low', 'mid', 'midhi' and 'hi'. Each dimension was then aggregated into hourly intervals. The mean of all Temperature/ Humidity/ Pressure values within a given hourly interval was calculated and substituted by its respective bin label. In addition, the difference between the first and the last Temperature/Humidity/Pressure value within a given hourly interval was calculated and substituted by its respective bin label, where the bins were calculated from the distribution of hourly differences. These bins labeled 'down2', 'down1', 'no', 'up1', 'up2' indicated the speed of change for each of the three dimensions Temperature/ Humidity/ Pressure in a given hour. This discretization process produced an hourly environmental data timeseries of six dimensions that only contained the labels defined above. The final dimension names were defined as: Temperature level, temperature change, humidity level, humidity change, pressure level, pressure change.

$$E := \left(y_i^{(TempL)}, y_i^{(TempC)}, y_i^{(HumL)}, y_i^{(HumC)}, y_i^{(PresL)}, y_i^{(PresC)} \right)_{(i=0..N)}$$

5.2 - Processing plant and control electrophysiology data

For a given plant/control the E1 electrode voltage timeseries $X := x_{i=0...N}$ spanning the entire recording period was processed as follows. A constant c>0 was added to X to make all values positive. The resulting series was then normalized by componentwise logarithm and subtraction of the first component's log to:

$$\log(X) - \log(x_0)$$

Next, a stepwise discrete fourier-transfom (DFT) without overlaps was calculated on the normalized X using a window length of 512 samples (~ 34 minutes of data). Windows extending over the border of a recording session were discarded. For each such window the DFT result vector of 512 complex values was first transformed to real values by using the complex Modulus, then the second half as well as the first value of each window were discarded, leaving a vector of length 255. Furthermore the log was applied again to every vector component and by combining the output vectors of all windows, the data processing resulted in a multivariate timeseries of 255 dimensions with hourly timestamps for each plant/control where each dimension corresponded to a frequency bin of bandwidth 0.0005 Hz in the frequency range between 0.5 mHz and 125 mHz.
Blind source separation was then performed on the multivariate timeseries for every plant/ control by applying Independent Component Analysis (R Version 4.2.2 statistical software; package fastICA Version 1.2-5.1). The ICA method is predominantly used in neuroscience to separate multichannel electrical recordings into a smaller number of independent and maximally non-gaussian components for the purpose of dimensionality reduction. To determine a suitable number of target components, heuristics were used to assess the featurespaces resulting from ICA decompositions for several values between 3 and 127 and the number of target components was fixed to 17. This resulted in a dimensionality-reduced representation of every plant/control by a hourly timeseries of 17 dimensions.

$$P := \left(x_i^{(P1)}, x_i^{(P2)}, \ldots, x_i^{(P17)} \right)_{(i=0..N)}$$

6 - Analysis: Finding associations between environmental and plant electrophysiology data

For a given plant, the previous dataprocessing steps led to a multidimensional timeseries that characterized a plant's state on an hourly basis through a numerical vector of length 17 (5.2). Likewise the environmental conditions the plant was finding itself in during the recording period were characterized by a six-dimensional timeseries of labels (5.1). To find associations between environment and plant/control we proceeded with fitting generalized linear models (R function glm) to the timeseries data.

$$E \sim GLM(P)$$

We used all the dimensions of the plant timeseries as independent variables and chose the dependent variable from the dimensions of the environmental timeseries. This approach may seem counter-intuitive, since we predict environmental variables with plant variables. However, because of the richness of the plant latent space in comparison to the environmental latent space our chances of discovering meaningful associations between the two is greater if we conduct the analysis this way. If a strong association between a plant electrical reaction and a specific environmental condition exists it would be possible to find a well-fitting gl-model.

6.1 - Motivation for using forward-looking analysis:

When compared to animals, most plants' reactions to environmental changes are slow and can take minutes or hours to manifest. In order to increase the chances of discovering delayed or slow onset plant electrical reactions, our analysis of plant data took a forward-looking approach. When searching for assocations with a given environmental condition prevalent at time t_0 we looked at plant data for time t_0 but also included plant data for times $t_1 < t_2 < t_3 < t_4$. Under the assumption that plants may react to environmental change with an unknown delay, we would then be able to identify an association, if one existed.

6.2 - Use of symbolic variable-value terms for describing subsets of environmental conditions:

After binning (5.1) each of the six environmental dimensions had a range of five possible values. We opted to use simple (size 1) and complex (size 2) variable-value pairs to further subset the environmental conditions encountered during the experiment.

Examples of simple (size 1) variable-value terms and their definition:

TempL.high	$:\Leftrightarrow y^{(TempL)} = high$
TempC.down2	$:\Leftrightarrow y^{(TempC)} = down2$
HumL.mid	$:\Leftrightarrow y^{(HumL)} = mid$
PresC.up1	$:\Leftrightarrow y^{(PresC)} = up1$

Examples of complex (size 2) variable-value terms and their definitions:

TempL.high and HumC.down1	$:\Leftrightarrow (y^{(TempL)} = high) \wedge (y^{(HumC)} = down1)$
PresC.up1 and TempC.up1	$:\Leftrightarrow (y^{(presC)} = up1) \wedge (y^{(TempC)} = up1)$

6.3 - Fitting gl-models to discover associations between environmental and plant variables

Examples of associations described by simple left-hand-side (LHS) terms of size 1:

$$y_{t0}^{(TempL)} = high \Leftrightarrow GLM\left(x_{t0}^{(P1)}, \ldots, x_{t0}^{(P17)}, x_{(t0+1)}^{(P1)}, \ldots, x_{(t0+1)}^{(P17)}, \ldots, x_{(t0+4)}^{(P1)}, \ldots, x_{(t0+4)}^{(P17)}\right) = 1$$

$$y_{t0}^{(HumC)} = down1 \Leftrightarrow GLM(\ldots) = 1$$

$$y_{t0}^{(PresL)} = mid \Leftrightarrow GLM(\ldots) = 1$$

Example of an association described with a complex LHS term of size 2:

$$\left(y_{t0}^{(TempL)} = high\right) \wedge \left(y_{t0}^{(PresC)} = down2\right) \Leftrightarrow GLM(\ldots) = 1$$

By our definition the dependent variable in these two types of LHS terms is binary and consequently all fitted gl-models were binary classifiers. We tested all possible LHS terms of size 1 (30 terms) and size 2 (375 terms) against all plants and control. Terms of size 3 or higher were not tested since the number of datapoints for each such term was too small to give significant results. For every term and plant/control combination we used out-of-sample k-fold validation (2<= k <= 5) to calculate a ROC/AUC value for the fitted gl-model. Briefly, the AUC (Area Under the Curve) measures the predictive performance of a binary classifier. Its values fall between 0 and 1.0. A value of 0.50 or less indicates that the model performs no better then random and a value of 1.0 means that the models predictions are perfect. Values above 0.60 indicate acceptable, non-random predictive performance.

6.4 - Selection of environmental subset terms most likely to reflect an association between plant and environment

Three conditions had to be met in order to include a simple or complex term into the final selection. The AUC value of its corresponding gl-model in the control experiment had to be less than 0.60 (control predictive quality is random), the number of test cases in the control experiment had to be at least 50 (significance) and the mean AUC over all plant experiments had to be greater than 0.60 (plant predictive quality is not random). This led to the selection of 3 simple terms (Table C1) and 13 complex terms (Table C2).

Results

Out of the selected subsets of (simple) environmental conditions (Table C1) the first (mean auc 0.73) strongly supports an association between high temperature and a recognizable plant electrical signalling pattern over the four hours following the onset of high temperatures, while the second (mean auc 0.65) supports an association between a fast drop in temperature, independent of the temperature level, and a specific plant electrical signalling pattern over the following four hours.

Of the 13 selected subsets of (complex) environmental conditions (Table C2) the first (mean auc 0.66) supports a recognizable plant signalling pattern following a fast decrease in temperature when paired with a fast rise in humidity, while the second one (mean auc 0.66) supports a recognizable signalling pattern following a slow decrease in temperature when paired with constant humidity that is neither low nor high. The remaining 11 subsets (0.65 >= mean auc >= 0.61) support that a variety of other environmental conditions are

followed by recognizable plant signalling patterns. Low temperature levels are present in six of those subsets, which suggests that low temperatures play a role but one that may vary in importance between plant species, while the previously discussed subsets of environmental conditions are likely important to all plant species.

Discussion

The results establish a link between specific environmental conditions and time-delayed plant electrical signalling patterns. We have used the expression 'association' to describe this link. Our methodology was not designed to prove a causal relationship between the two since this would require a different type of experimental design with strict control of environmental variables and that can only be achieved in laboratory or greenhouse settings but not in the wild. However, given that plants are known to react and adapt to a variety of external stimuli, a causal effect of the environment on the tested plants is so far the most likely explanation for the associations discovered with our methodology.

In our view the two most interesting associations are (1) the simple one involving high temperatures to which all plants appear to be sensitive and (2) the complex one involving a fast drop in temperature combined with a quick rise in humidity. The latter is equivalent to a sudden decrease of Vapor Pressure Deficit (VPD) which is an important measure related to plant water stress that appears to elecit an immediate response in all plants.

Our methodology used extracellular electrical voltage measurements on plants in combination with data analysis techniques derived from neuroscience to nondestructively identify and characterize plant reactions and plant internal states. For future studies, substituting the general linear models we have used in this study by neural neural network models will likely improve the identification and characterization of environmental conditions and other external factors that impact a plant. We believe that our findings are a useful addition to the methods and tools available in plant biology in general and plant electrophysiology in particular since they enable researchers to use plant electrical reactions in near realtime for the characterization of otherwise difficult to observe plant state changes in response to external stimuli.

Author contributions

S.W. conceptualized and designed the study, performed the field experiments, conducted the data analysis, interpreted the data and drafted the manuscript. The following provided manuscript revisions: (tbd)

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Figures:

Table M1 - Plant species and recording periods

Plant	*Duration of Recording*	*Date Start/End*
Spruce (P. Abies)	32 weeks	Feb 2023/Oct 2023
Larch (L. Decidua)	19 weeks	Jan 2024/Jun 2024
Yew (T. Baccata)	36 weeks	Nov 2022/Aug 2023
Birch (B. Pendula)	20 weeks	Jan 2024/Jun 2024
Olive (O. Europea)	20 weeks	Mar 2024/Aug 2024
Magnolia (M. Soulangeana)	18 weeks	Apr 2024/Aug 2024
CONTROL	10 weeks	Sep 2024/Nov 2024

Table C1 - Environment size 1 terms, mean AUC (all plants), AUC (control), AUC (by plant)

Environment Term1	All plants *Mean Auc*	*Control Auc*	*Spruce Auc*	*Birch Auc*	*Olive Auc*	*Larch Auc*	*Magnolia Auc*	*Yew Auc*
TempL.hi	**0,73**	0,47	0,85	0,70	0,72	0,82	0,64	0,62
TempC.down2	**0,65**	0,50	0,77	0,64	0,59	0,74	0,59	0,57
TempC.no	0,62	0,53	0,74	0,61	0,57	0,66	0,54	0,58
PresL.verylow	0,60	0,52	0,62	0,57	0,66	0,55	0,57	0,65
HumL.midhi	0,60	0,50	0,64	0,52	0,60	0,65	0,62	0,55
TempC.down1	0,59	0,52	0,64	0,54	0,60	0,59	0,64	0,56
HumL.low	0,59	0,52	0,63	0,57	0,54	0,66	0,54	0,60
PresL.midhi	0,58	0,50	0,61	0,55	0,60	0,57	0,59	0,57
PresC.up2	0,58	0,51	0,67	0,56	0,58	0,59	0,54	0,55
PresC.down2	0,57	0,55	0,59	0,53	0,62	0,53	0,58	0,55
PresL.mid	0,57	0,51	0,58	0,54	0,61	0,54	0,52	0,60
TempC.up1	0,57	0,51	0,60	0,58	0,55	0,56	0,55	0,54
HumC.down1	0,55	0,52	0,61	0,53	0,52	0,55	0,53	0,55
PresC.up1	0,53	0,51	0,55	0,53	0,55	0,51	0,52	0,53
PresC.no	0,52	0,50	0,54	0,52	0,52	0,51	0,51	0,53

Table C2 - Environment size 2 terms, mean AUC (all plants), AUC (control), AUC (by plant)

Environment Term1	AND Term2	All plants Mean Auc	Control Auc	Spruce Auc	Birch Auc	Olive Auc	Larch Auc	Magnolia Auc	Yew Auc
TempC.down2	HumC.up2	**0,66**	0,58	0,79	0,65	0,59	0,77	0,58	0,58
TempC.down1	HumL.mid	**0,66**	0,56	0,71	0,64	0,65	0,65	0,70	0,62
TempC.no	HumL.mid	**0,65**	0,54	0,72	0,58	0,67	0,67	0,63	0,64
HumL.midhi	PresL.verylow	**0,65**	0,57	0,62	0,59	0,72	0,74	0,61	0,61
HumC.no	HumL.midhi	0,63	0,50	0,72	0,59	0,61	0,65	0,63	0,56
TempL.low	HumC.no	0,62	0,54	0,68	0,61	0,60	0,61	0,62	0,62
TempC.no	HumL.midhi	0,62	0,50	0,73	0,58	0,59	0,59	0,67	0,56
TempL.low	HumL.midhi	0,62	0,50	0,63	0,66	0,59	0,59	0,64	0,62
TempC.no	TempL.low	0,62	0,50	0,64	0,71	0,56	0,65	0,57	0,57
TempC.no	PresL.verylow	0,61	0,57	0,62	0,55	0,56	0,58	0,63	0,73
TempC.up1	TempL.low	0,61	0,50	0,66	0,62	0,58	0,64	0,58	0,56
TempC.down1	TempL.low	0,61	0,57	0,67	0,58	0,65	0,59	0,58	0,58
TempL.low	HumC.down1	0,61	0,54	0,66	0,56	0,58	0,64	0,58	0,61
TempL.low	PresL.verylow	0,59	0,56	0,59	0,54	0,56	0,57	0,61	0,68
HumC.down1	HumL.midhi	0,59	0,48	0,62	0,53	0,56	0,61	0,65	0,57
TempC.no	HumC.no	0,59	0,58	0,72	0,55	0,51	0,65	0,55	0,56
TempL.low	HumL.mid	0,59	0,56	0,60	0,54	0,59	0,54	0,64	0,61
HumC.down1	PresL.verylow	0,59	0,50	0,60	0,53	0,64	0,56	0,55	0,64
TempL.low	PresC.up1	0,58	0,53	0,58	0,60	0,58	0,59	0,57	0,58
TempC.up1	HumL.mid	0,58	0,53	0,62	0,54	0,56	0,59	0,55	0,61
TempL.low	PresL.low	0,58	0,56	0,59	0,60	0,57	0,55	0,55	0,61
HumL.mid	PresL.low	0,58	0,53	0,67	0,53	0,57	0,57	0,53	0,58
HumC.down1	HumL.mid	0,57	0,55	0,65	0,52	0,58	0,55	0,53	0,58
HumL.midhi	PresC.up1	0,57	0,54	0,54	0,55	0,62	0,60	0,54	0,55
HumL.mid	PresC.no	0,57	0,57	0,58	0,57	0,53	0,57	0,55	0,60
TempL.low	PresC.no	0,56	0,54	0,61	0,53	0,56	0,58	0,54	0,52