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# Hydraulic conductance of root and shoot measured with the transient and dynamic modes of the high-pressure flowmeter

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**Abstract** – The hydraulic conductance ( $k$ ) of shoots and root systems was measured using the transient and the dynamic modes of the high pressure flowmeter (HPFM). Measurements were conducted on *Quercus robur* and *Fagus sylvatica* plants grown on different substrates (forest soil, sand, Terra-green and vermiculite) and harvested at different times of the year. The values of  $k$  obtained by the transient mode were compared to those obtained by the dynamic mode. A tight 1:1 correlation was observed for shoots and defoliated stems but several types of discrepancies appeared for root systems. The underestimation of  $k$  by the dynamic mode as compared to the transient mode could be explained by reverse osmosis at the endodermis. However the transient mode was not functional for some root systems. This problem occurred essentially in small plants harvested early in the year before budbreak had been completed. Nature and origins of problems are discussed.

**hydraulic conductance / high pressure flowmeter / transient mode / root / shoot**

**Résumé** – Mesure de la conductance hydraulique des parties aériennes et des systèmes racinaires avec les modes transitoire et dynamique du fluxmètre haute pression. La conductance hydraulique des parties aériennes et des systèmes racinaires a été mesurée avec le fluxmètre haute pression (HPFM) en mode transitoire et en mode dynamique. Les mesures ont été effectuées sur des plants de *Quercus robur* et de *Fagus sylvatica* ayant poussé sur différents substrats (sol forestier, sable, Terra-green, vermiculite) et récoltés à différentes périodes de l'année. Les valeurs de  $k$  obtenues par le mode transitoire ont été comparées à celles obtenues par le mode dynamique. Une bonne corrélation 1:1 a été observée pour les rameaux et les tiges défeuillées mais plusieurs types de divergence sont apparus pour les systèmes racinaires. La sous-estimation de  $k$  par le mode dynamique par rapport au mode transitoire peut être expliquée par l'osmose inverse. Cependant le mode transitoire n'était pas fonctionnel pour certains systèmes racinaires. Ce problème s'est produit essentiellement pour des petits plants récoltés tôt dans l'année, avant que le débourrement ne soit fini. La nature et l'origine des problèmes sont discutées.

**conductance hydraulique / fluxmètre haute pression / racine / rameau / mode transitoire**

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## 1. INTRODUCTION

According to the Ohm's law analogue, the water status of a plant is controlled by the soil water availability and the hydraulic properties of the pathway used by the water flow from soil to the atmosphere [2, 26]. The importance of investigating hydraulic properties of trees is highlighted by recent studies showing that they may play a role in ecological strategies of species and that they can underlie the response to environmental changes [5, 10]. For instance, pioneer species like *Acer saccharinum* and *Juglans regia* were vulnerable to cavitation, exhibited hydraulic segmentation and showed high hydraulic conductance ( $k$ ), whereas established species like *Quercus species* and *Pinus contorta* were less vulnerable and presented a relatively low  $k$  [23]. Drought stress can significantly reduce xylem  $k$  through cavitation [1, 17] and also may affect root hydraulic conductivity by increasing the deposition of hydrophobic substances like suberin [8, 11]. Moreover, the relative contribution of plant compartments to the hydraulic resistance varies from one species to another. Indeed, the contribution of the root system to the whole plant resistance ranges from 20 to 90% [23 and references therein]. Effects of drought on root hydraulic conductivity will then have different consequences on whole hydraulic resistance and on leaf water potential depending on species.

Several techniques have been developed to measure  $k$ . The more conventional one is the evaporative flux method where  $k$  is calculated from the ratio of the evaporative flow over the water potential gradient it induces [3, 7, 28]. It can be used for mature trees as well as for small potted plants. This technique allows also the estimation of the  $k$  of roots (plus xylem) when considering the water potential gradient between the soil and a non-transpiring leaf [24]. Specific techniques were also developed to measure  $k$  of roots: the pressurisation of root systems [6], the root pressure probe [18], the potometer [29], the negative pressure flow system for root sections [14], the high pressure flowmeter (HPFM) [25, 27]. Each method was developed for a particular purpose and presents its own advantages and inconveniences. The evaporation flux method is not destructive and also includes the soil-root interface resistance but lacks accuracy. The root pressure probe can be used on a single root as well as on a whole root system and the water potential gradient imposed to the roots can have an osmotic or hydrostatic nature. Potometers allow to get the resolution of the single root keeping the integrity of the plant. The negative flow pressure on root sections allows a fine dissection of hydraulic

properties along roots and thus helps in spatial modelling of water uptake [4].

The HPFM is rapid and easy to use in laboratory as well as in field experiments and it can also be used to measure  $k$  of shoot. It consists of perfusing water in the root system or in the shoot while recording flow and pressure;  $k$  is calculated from the linear regression slope of flow versus applied pressure. It should be noticed that xylem vessels are refilled by the high pressure water perfusion and thus that HPFM measures the maximum hydraulic conductance. HPFM presents several operating modes: quasi-steady state, dynamic or transient. For root systems, where water flows in the opposite direction to the transpiration stream, studies comparing the different modes of the HPFM revealed some difficulties when measuring root hydraulic conductance ( $k_r$ ) [25, 27]. Considering different problems such as solutes accumulation in the xylem due to reverse flow, bubble compression or elastic behaviour of roots, it was concluded that the transient mode of the HPFM was the best solution to measure  $k_r$ .

In this paper, we present data of hydraulic conductance of root systems, shoots and stems measured with HPFM using the transient and the dynamic-step modes consecutively. Measurements were conducted on two species with plants grown on different substrates, covering a large range of sizes and harvested at different times of the year. The purpose of this study was to answer the following questions: Are discrepancies between data obtained by the two modes found only for root systems? Is the transient mode efficient for root systems in any case? If not, what are the reasons responsible for the observed difficulties?

## 2. MATERIALS AND METHODS

### 2.1. Plant material and growth conditions

Data are issued from 3 different batches of plants. The first batch of data was obtained from an experiment conducted during 1998 on *Quercus robur* L. Acorns were sowed in February in 5-liter pots filled with sandy soil (B-horizon) from the Mondon forest (North-East of France) and seedlings were grown for 5 months in a greenhouse where temperature remained over 16 °C. Seedlings were harvested in July when they were  $0.75 \pm 0.36$  m high. The second batch of data was obtained from an experiment conducted on one-year old *Q. robur* L. and

*Fagus sylvatica* L. Seeds were planted in July 1998 in 3.5-liter pots filled either with calibrated sand (2–3 mm) or with Terra-green (calcinated clay aggregates) and seedlings were grown in a greenhouse. Measurements were conducted during 1999, all over the second year of growth, from before budbreak to after leaf-fall, covering a large range of sizes (0.1–0.9 m height for both species) and different physiological states. The last batch of data was obtained from an experiment conducted on one-year old *F. sylvatica* L. plants. Seeds were planted in 3.5-liter pots filled with vermiculite in August 1999, were grown in greenhouses at either 350 or 700  $\mu\text{mol mol}^{-1}$   $\text{CO}_2$  and were harvested in July 2000 when they were from 0.30 to 0.65 m high. In the three studies, plants were supplied with complete slow-release fertiliser (Nutricote T100, NPK 13/13/13, 4g  $\text{L}^{-1}$  of substrate) and were well-watered.

## 2.2. $k$ measurements

Plants were brought into the laboratory the evening before measurements, were watered and, for leafed plants, were covered with a black plastic bag until measured. In some plants, a positive hydrostatic pressure in the xylem was observed when cutting shoots from root systems just before measurement (exudation). This was due to the loading of the xylem with nutrients which increased its osmotic pressure. Shoots were cut about 40 mm above the soil surface and kept until measurement covered by a plastic bag with the collar plunging in water. Root systems were flooded in the pot without removing it from the substrate and connected to the high-pressure flowmeter (HPFM) [27]. Filtered distilled water was forced to flow through the root system (flow was opposite to transpiration stream) under increasing pressure and the hydraulic conductance ( $k$ ) was calculated from the slope of the plot water flux ( $F$ ) versus pressure ( $P$ ):

$$k = \Delta F / \Delta P.$$

The hydraulic conductance of the root system ( $k_r$ ) was measured twice, using two different modes consecutively. The first mode consisted of increasing pressure to 0.5 MPa with a constant rate of 5–8  $\text{kPa s}^{-1}$  while measuring  $F$  and  $P$  every 3 s and was called “transient mode” by Tyree and coworkers (1995).  $k_r$  was computed from the slope of the last 8 points (corresponding to the range 0.4–0.5 MPa where the regression is linear; in the range of lower pressure, the curve may be disturbed by an extra flow due to bubble compression). The second mode consisted of increasing pressure by steps of 0.1 MPa every 3 minutes to a maximum of 0.5 MPa and was called

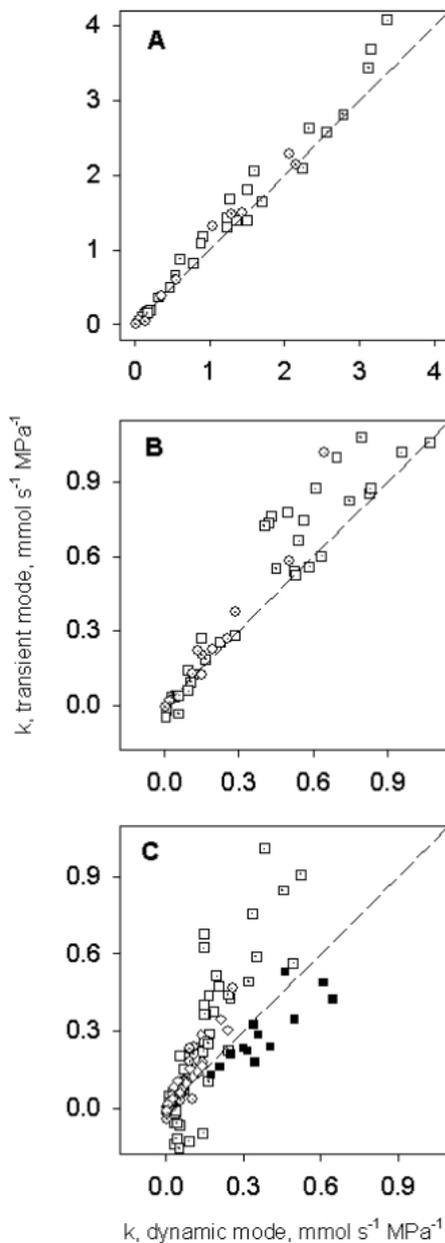
“dynamic mode”. Flow and pressure were recorded at the end of each step once the flow was quasi-stable.  $k_r$  was calculated from the linear regression over the whole range of pressures. Measurements were first done with the transient mode (3 to 5 consecutive measurements) and then with the dynamic mode except for the first batch of plants (1998) for which it was the opposite.

After the measurement of  $k_r$ , the shoot was connected to the HPFM and measurements were conducted with the transient mode until plots were superposed (usually 3 replicates were sufficient). Then the hydraulic conductance of the shoot was measured with the dynamic mode. Leaves were then removed and the same procedure was applied to the defoliated stem. The hydraulic conductance of shoot and stem ( $k_{\text{sh}}$  and  $k_{\text{st}}$  respectively) was measured by both modes only for the second batch of plants.

## 3. RESULTS

Almost all values of shoot hydraulic conductance ( $k_{\text{sh}}$ ) obtained with the dynamic mode were equal to those obtained on the same shoot with the transient mode over the whole range of data, from 0.05 to 1.0  $\text{mmol s}^{-1} \text{MPa}^{-1}$  (figure 1B). However, for some of the largest plants, the transient mode tended to yield higher values than the dynamic mode. Since shoots were not pressurised before measurement, it may be that the transient mode overestimated  $k$  due to an uncomplete evacuation of air in the leaf tissue and that it was not the case anymore for the dynamic mode as water had already been perfused through the shoot for longer. For the hydraulic conductance of the defoliated stems, values ranged from 0.05 to 4  $\text{mmol s}^{-1} \text{MPa}^{-1}$  and the correlation between the two modes was in this case almost perfect (figure 1A).

The comparison of the hydraulic conductances of root systems ( $k_r$ ) obtained by the two modes of HPFM displayed more discrepancies (figure 1C). Whatever the species and the substrate, when the transient mode was applied first, it yielded higher values of  $k_r$  than did the dynamic mode. Moreover, the larger the root system was, the larger was the deviation from the 1:1 correlation. However when the order of application of the two modes was inverted (for plants of batch 1, *Q. robur* on forest soil), the dynamic mode yielded slightly higher values of  $k_r$  than the transient mode. Another problem was the record of negative correlations between flow and pressure with the transient mode for some small root systems



**Figure 1.** Hydraulic conductance measured with the transient mode versus hydraulic conductance measured with the dynamic mode for (A) defoliated stems, (B) whole shoots and (C) root systems. Data were obtained from 3 batches of plants with different species and different substrates. Batch 1: ■ *Q. robur* on forest soil; batch 2: □ *Q. robur* on sand, □ *Q. robur* on Terra-green, ○ *F. sylvatica* on sand, ⊙ *F. sylvatica* on Terra-green; batch 3: ◇ *F. sylvatica* on vermiculite. The dotted line represents the 1:1 regression. Except for batch 1, measurements with the transient mode were made before measurement with the dynamic mode.

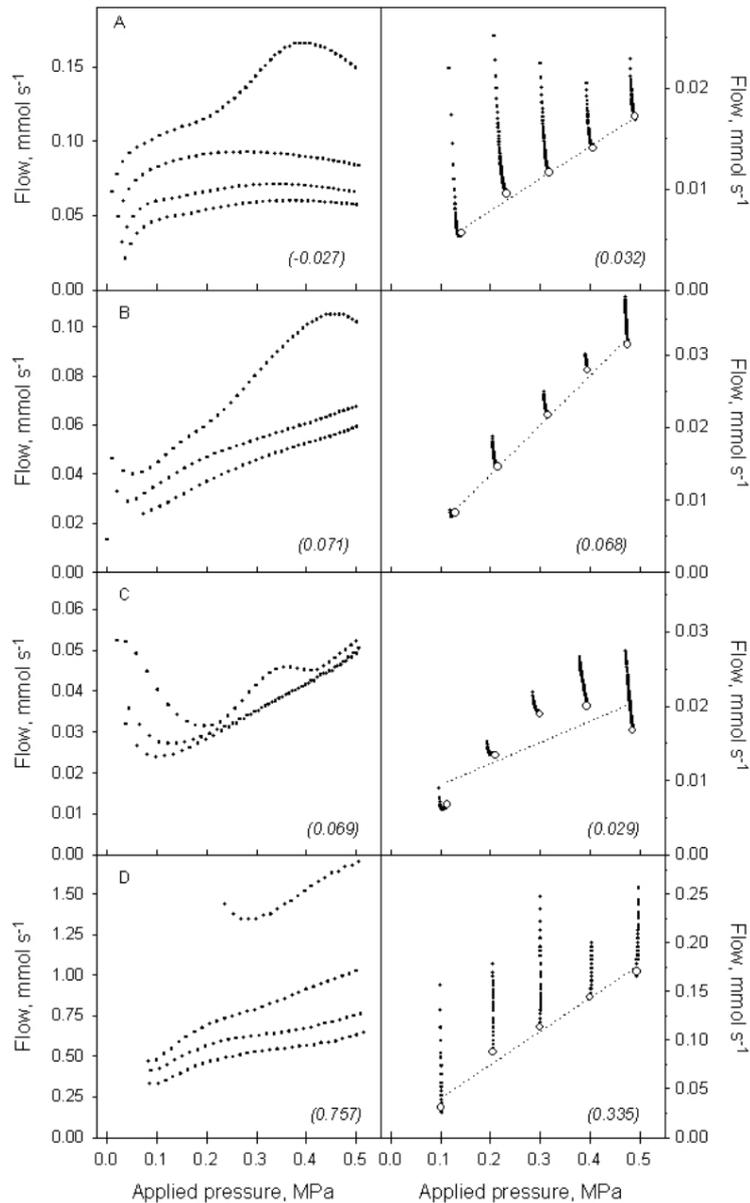
resulting in negative values of  $k_r$  (figure 1C). These negative values made no sense in term of hydraulic conductance but showed that the transient mode was inefficient to measure  $k_r$  for these small root systems.

Typical time courses of flow versus pressure during the measurements are presented in figure 2. For each plant,  $k_r$  was measured first with the transient mode (left column) and then with the dynamic mode (right column). The first pair of graphs illustrates the case where the transient mode did not allow  $k_r$  measurement while the dynamic mode led to linear correlation between flow and pressure (figure 2A). The frequency of occurrence of this case and the parameters of the situations are described in table 1. For *Quercus robur*, it did not happen to plants grown on forest soil, happened rarely to those grown on sand (4%) but happened to 36% of those grown on Terra-green. Moreover, 93% of these last cases corresponded to plants harvested early in the season, when budbreak index was inferior or equal to 3 (corresponding to the opening of buds). For *Fagus sylvatica*, it did not occur to plants grown on vermiculite but happened with about the same frequency to those grown on sand and on Terra-green (36 and 42%). As for oak, most of the cases corresponded to plants which were harvested before the budbreak had been completed. Concurrently, for some root systems of approximately the same size and in the same range of  $k_r$ , both modes yielded similar values of  $k_r$  (figure 2B).

The third type of time course is presented in figure 2C: transient curves were very repeatable while the dynamic mode yielded a classical positive correlation between flow and pressure for the first steps but then showed a decrease of flow with further increasing pressure. This was probably a time dependent reaction due to reverse osmosis [27]. For larger root systems and higher  $k_r$ , both modes of measurement led to a tight correlation between flow and pressure with regression coefficients  $r^2$  higher than 0.95 (figure 2D). However, when the transient mode was used first, values of  $k_r$  were always higher than those obtained by the dynamic mode (figures 1C and 2D). Moreover the discrepancy between the two modes increased with increasing  $k_r$ .

#### 4. DISCUSSION

The high pressure flowmeter (HPFM) is recognized as a rapid, easy and reliable method to measure the hydraulic conductance ( $k$ ) and is now widely used [2, 12, 24].



**Figure 2.** Typical time courses of water flow versus applied pressure during the measurement of root system hydraulic conductance with the HPFM using the transient mode (left column) and the dynamic mode (right column). Flow and pressure were recorded every 3 s, each point corresponds to one record. For the transient mode, pressure was increased at a rate of 5–8 kPa s<sup>-1</sup> and  $k_r$  was estimated from the slope of the last 8 points. For dynamic mode, pressure was increased to the next step after 3 min at a given level, once the water flow was quasi-stable and  $k_r$  was calculated from the slope of the regression of the 5 points corresponding to the last recording of each step (open circle) if  $r^2$  was higher than 0.95. For each plot,  $k_r$  is given between brackets (mmol s<sup>-1</sup> MPa<sup>-1</sup>).

The mean root hydraulic conductance ( $k_r$ ) obtained with the HPFM on the 5 month-old oak seedling of batch 1 was comparable to these obtained by root system pressurisation on the same plants:  $0.29 \pm 0.11$  and

$0.36 \pm 0.17$  mmol s<sup>-1</sup> MPa<sup>-1</sup> respectively (data not shown), validating our measurements with the HPFM. Moreover, when  $k_r$  was standardised by root surface area, the mean root hydraulic conductivity ( $Lp_r$ ) was

**Table 1.** Frequency of occurrence of the impossibility to measure  $k_r$  with the transient mode of the HPFM (negative correlation between flow and pressure) as a function of the growth substrate and the state of budbreak. Budbreak index (BI) = 3 corresponds to the emergence of first leaves from the bud.

Number of plants	<i>Q. robur</i>			<i>F. sylvatica</i>		
	Soil	Sand	Terra-green	Sand	Terra-green	Vermiculite
Total	25	23	41	11	38	28
with negative slope	0	1	15	4	16	0
with $BI \leq 3$	–	10	21	9	25	–
with $BI \leq 3$ and negative slope	–	1	14	4	12	–

$1.02 \pm 0.41 \text{ mmol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$  (data not shown) which was close to values obtained with the root pressure probe on plants of same species and similar age: from 0.4 to  $1.4 \text{ mmol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$  [20]. Similarly for *F. sylvatica* plants of batch 3,  $Lp_r$  was  $0.58 \pm 0.17 \text{ mmol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$  (data not shown), which is comparable to  $0.19\text{--}0.43 \text{ mmol s}^{-1} \text{ MPa}^{-1} \text{ m}^{-2}$  found on 6 month-old beech [19].

Except for some of the largest plants, the hydraulic conductance of the shoots measured with the transient mode of the HPFM was very close to that measured with the dynamic mode. Since shoots were not pressurised before measurement, the good agreement between the two modes indicates that stopping transpiration by covering plants brought them back to a high water potential and that xylem and leaf tissues were resaturated by the few transient flushes. However, for plants with a high level of embolised vessels or for large shoots, a previous pressurisation may be necessary to fully resaturate vessels before measurement of  $k$  with the transient mode. This pre-treatment may not be sufficient: Nardini and Tyree [13] compared the transient mode to the quasi-steady state mode (where 0.3 MPa is applied until flow becomes quasi-constant) on *Quercus rubra* shoots. They found an overestimation of  $k_{sh}$  by the transient mode, increasing with shoot size, and suggested that bubbles in xylem and leaves, far from the water injection point (collar), were not completely evacuated by the previous pressurisation.

For most of our measurements, root hydraulic conductance was higher when measured by transient mode than by dynamic mode whatever the species and the substrate. The easiest explanation of this discrepancy is the underestimation of  $k_r$  by the latter due to reverse osmosis [27]. Since the root system presents properties of a semi-permeable membrane [9, 22], the perfusion of water for a long time in the opposite way to the transpiration flow

concentrates the initially diluted solutes of xylem sap in the xylem of small absorbing roots, thus creating an increasing osmotic counter force to the hydrostatic pressure [25]. For some plants, reverse osmosis was very easy to detect (figure 2C) but could also be less evident (figure 2D). If this phenomenon is strongly expressed (flow decreases although pressure increases), it is easily recognised but it may be only slightly present and therefore leads to  $k_r$  underestimation. Stopping transpiration by covering shoots before measurement could have amplified this phenomenon. Since the transient mode takes less than 90 s for the measurement, the xylem osmotic pressure does not vary significantly and  $k_r$  should be correctly estimated by the slope of the  $F$  versus  $P$  regression. Moreover, it has been validated by methods where water flows in the “right” direction and where no solutes accumulation occurs (pressurisation of the root system, evaporative flux) [25, 28]. It is thus presented as the best solution to measure  $k_r$  as compared to quasi steady state or dynamic modes [25, 27] and now widely used [13, 24]. Strangely, for the batch of plants where the dynamic mode was applied first, it yielded slightly higher values of  $k_r$  than did the transient mode. According to the reverse osmosis hypothesis, the order in which the two different modes are applied should not affect the expected underestimation of  $k_r$  by the dynamic mode. Either no solute accumulation occurred (very low solute concentration in the xylem sap) and  $k_r$  was correctly estimated by the dynamic mode or the transient mode also underestimated  $k_r$ . This could happen for instance if the volume of air in the root was important and not easily pushed out. The water flow compressing air bubbles would remain significant as compared to the water flow crossing the root system and diminishing in the range of pressures where the linear regression is calculated. The slope of the regression between recorded water flow (the sum of both) and pressure would then be reduced.

We also met cases where the transient mode was inefficient to measure  $k_r$ . For some root systems, the slope of  $F$  versus  $P$  remained negative even after several flushes. Several different studies comparing the transient mode of the HPFM to other techniques revealed a good agreement between data, validating this method [23–25, 28]. To our knowledge, such difficulties as found in the present study have never been mentioned. We suggest that the conductance of the root system was so low that the water flow needed to compress air bubbles in the xylem or in the root tissue was higher than the water flow crossing root system. This hypothesis is supported by the efficiency of the dynamic mode where a tight linearity was observed between  $F$  and  $P$ . If we consider that the radial hydraulic resistance of roots is not only due to endodermis but is evenly distributed over the entire root tissue [15, 21], air in the root cortex may also have contributed to this elastic perturbation of the measurement. It happened essentially with plants of small size and early in the season, before break was completed. In these species, after the winter break, root growth is concomitant to aerial development [16] and a high proportion of old root tissue may lead to a high elasticity of the root system. For oak plants, it occurred essentially to root systems grown in Terra-green, therefore substrate may have induced changes to root anatomy such as development of aerenchyma. However inefficiency of the transient mode also occurred for large root systems of plants harvested in the middle of the summer (Barigah, pers. comm.). This indicates that there could be other reasons than size and physiological state which induce the situation where  $k_r$  can not be estimated using the transient mode.

As compared to other techniques, transient measurement of  $k$  with the HPFM is easy, rapid and can be used to determine hydraulic resistance of roots as well as of stem or leaves [23, 24]. We showed that for well-watered plants, transient measurement can be run with satisfaction on shoots even without pressurisation if plants were brought back to high water potential beforehand. Our data confirmed that the transient mode is preferable to measure the hydraulic resistance of root systems but also showed that there are some cases where it is not applicable. In particular, it failed for small plants harvested early in the season when hydraulic conductance was very low. In this case dynamic measurement may be used. However there remains a risk of underestimating  $k_r$  due to reverse osmosis.

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