

## WATER UPTAKE IN DECIDUOUS TREES DURING WINTER AND THE ROLE OF CONDUCTING TISSUES IN SPRING REACTIVATION

by

Sam. Essiamah and Walter Eschrich

Forstbotanisches Institut der Universität Goettingen, Buesgenweg 2, 3400 Goettingen, F.R.G.

### Summary

In winter, deciduous trees lack any means for transpiration, nevertheless their buds swell and increase in weight. It is known that vessels play an important role in spring reactivation and that phloem may be involved since buds fail to break when twigs are ringed. This study investigates water/nutrient translocation from winter until reactivation in spring for five North European species: maple (*Acer pseudoplatanus* L.), birch (*Betula pendula* Roth), alder (*Alnus glutinosa* Gaertn.), beech (*Fagus sylvatica* L.), and ash (*Fraxinus excelsior* L.). Accordingly emphasis is laid on the relative timing of onset of water conduction among the species.

Beginning in late March, a continuous increase of water movement occurs in all the trees. However, this began earlier in birch and maple than in beech. In ash water uptake is delayed. Similar results were obtained with transpiration experiments. Delay of water conduction in ash is probably because ring-porous species depend on new conducting tissues to replace the previous year's nonfunctioning xylem. Analysis of three cations in buds showed that magnesium remained constantly low while calcium gave high values from the beginning. Potassium concentration rose and its accumulation correlated with water content/dry weight increase during bud development. Potassium thus indicated acropetal transport to the buds, since the spring sap showed the same tendency.

**Key words:** *Acer*, *Betula*, *Alnus*, *Fagus*, *Fraxinus*, bud swelling, vessels, sap transport.

### Introduction

Transpiration and water uptake in woody plants during summer have been extensively studied. However, little is known about these phenomena in leafless deciduous trees during winter and spring (Iwanoff, 1924; Burström, 1948; Pollock, 1953; Huber, 1956).

This is surprising, since a basic requirement for the start of spring activities of deciduous trees is water for optimal hydrolysis of food storage macromolecules and for increased enzyme activities.

In this paper, water and nutrient transport in five common European tree species from winter

till reactivation in spring is reported. Measurements of transpiration were carried out on tree twigs to determine if excised shoots from deciduous trees are able to take up water. The dye ascent measurements also helped to time the onset of water conduction among the species.

Analysis of water and cation uptake in the buds was undertaken to test the hypothesis of Burström (1948) that uptake of water during bud development was linked to a pronounced increase in cation concentration.

The data will be discussed in relation to the role of the conducting tissues during spring reactivation.

### Materials and Methods

The investigation on water uptake was carried out with 2–5-year-old trees of maple (*Acer pseudoplatanus* L.), birch (*Betula pendula* Roth), alder (*Alnus glutinosa* Gaertn.), beech (*Fagus sylvatica* L.) and ash (*Fraxinus excelsior* L.). Seedlings, obtained from a tree-nursery, were cultivated as pot plants in the open and used for the tests between mid-January and the beginning of May.

Experiments were also conducted to measure transpiration of shoot samples giving additional information on water uptake during reactivation.

Since swelling buds were found to influence water uptake by shoots, a third series of tests were conducted to determine the water content of buds. Changes in bud cation concentration were also measured.

Material for these 2 series of experiments were obtained partly from the seedlings and partly from twigs of 36-year-old trees of the five species growing in forest stands already described (Essiamah, 1980).

### Dye-ascent measurements

At intervals of three days from mid-January up to the beginning of May, nine seedlings of each species were taken for measurement. Three specimens of each were taken in the morning, in the afternoon and in the evening. The pot of the seedling was briefly submerged in water, and the shoot was cut with a single-edge-blade transverse and smooth under water, and trans-

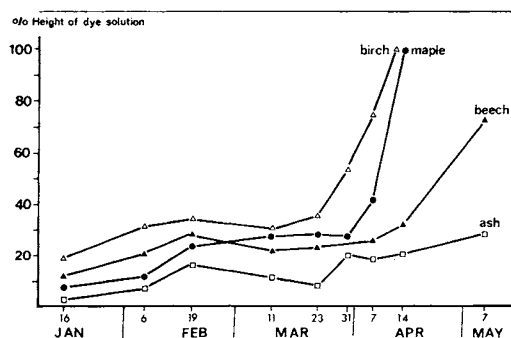


Fig. 1. Water uptake in shoots of birch, maple, beech and ash. Heights of dye-ascent after 15 minutes expressed as percentage of shoot length.

ferred quickly into a beaker with Amidoblack-solution (0.6%), acidified with a drop of acetic acid for stabilisation (Eschrich, 1976).

After 15 minutes, the immersed shoot-end was washed with water and the length of the entire shoot measured. The height of the ascended dye was found by cutting the shoot (shoot upwards) into one cm segments and by finding the front of the dye-solution with the help of a stereomicroscope. The shoot lengths ranged from 21–35 cm for maple, 13–25 cm of birch, and 28–40 cm for beech and ash.

#### Transpiration measurements

To determine water consumption, shoots of 10–15 cm length were used. The shoots were collected, weighed immediately, and their cut ends were immersed in a plastic vial containing 20 ml of water which was sealed against evaporation with Terostat (Teroson, Heidelberg, FRG). The whole setup was again weighed. The samples were maintained in a well ventilated room of 18–22°C and illuminated by daylight and continuous supplementary light from incandescent lamps (10 mw/cm<sup>2</sup>) delivered above the seedlings. Water uptake was determined by weighing the setup regularly. The experiments were conducted at varying intervals from twice a month to thrice per week before bud burst. Bud burst (bb in Fig. 2) is defined as the growth stage when young leaves just protrude beyond the bud.

#### Water and cation content in buds

Buds of maple, beech and alder were used for this investigation. To determine water content (wc), ten buds of each species were weighed, oven-dried at 100°C for 24 h and reweighed

(until constant weight was attained). Water content was expressed as percentage of dry weight. Along with water content measurements, the amounts of Ca<sup>++</sup>, Mg<sup>++</sup> and K<sup>+</sup> in buds were determined spectrophotometrically. For this purpose, the dried buds were ground in a mortar with pestle and passed through a 0.5 mm mesh sieve to obtain a homogeneous material. The material was subsequently stored in polyethylene bottles at -20°C.

Half-gram portions of bud powder were weighed into 50 ml Erlenmeyer flasks and wet-washed with a 12 ml conc. acid mixture of nitric, perchloric and sulphuric acids (8 : 2 : 1). Double-distilled water (ddw) was added to the digests which were filtered quantitatively into 25 ml graduated flasks and filled up to a standard volume with ddw. The concentration of cations was measured with a Perkin-Elmer 403 Atomic-Absorption Spectrophotometer after the 'bud standard solution' had been diluted 1 : 50 with ddw.

## Results

### Uptake and transport of dye solution

Transport experiments with Amidoblack solution were carried out during spring on maple, birch, beech and ash. The results are presented in Figure 1. Since the values are expressed as percentage of the shoot length, the relatively low rise in early spring should indicate water movement in the shoots.

From mid-January to mid-March, the ascent of dye remained relatively constant and did not exceed the 35% value. After March, when the buds started developing according to the characteristics of the species, a dramatic increase in

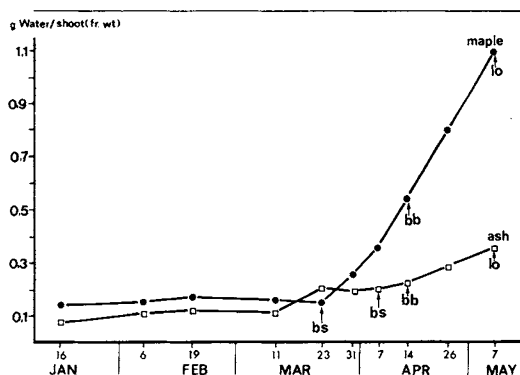


Fig. 2. Water loss by transpiration of maple and ash expressed as g water/shoot fresh weight/day; bs: bud swelling phase; bb: bud burst; lo: leaf out.

water uptake was recorded. Water uptake occurred earlier in birch and maple than in beech, although all three are diffuse-porous species. These data, however, reflect the developmental state of the tree species in nature, because birch and maple usually leaf out earlier than does beech. Ash, a ring-porous species, behaved differently. Water uptake which was observed in the diffuse-porous trees during early spring could not be recorded. The dye solution began to rise above the 20% value only when the buds started bursting on 14 April.

To find out if the degree of bud development influences water uptake in spring, further experiments were undertaken with beech shoots. Bud length and bud break were selected as criteria for growth, because external climatic data seemed less reliable as index for bud development. Water uptake in deciduous trees during spring appears strongly dependent on bud development. Water uptake rises progressively during late spring but only when the buds increase in size. This applies particularly to diffuse-porous tree. In ring-porous species, however, water uptake is delayed. Delay of water conduction in ash is probably because ring-porous species depend on new-conducting vessels to replace the previous year's non-functioning xylem.

#### *Transpiration analysis on shoots*

In this study shoot sampling of the investigated tree species commenced on 16 January and finished on 7 May. All shoots were exposed from the first to the fourth day to identical experimental conditions.

In Figure 2, the amount of water transpired by maple (diffuse-porous) and ash (ring-porous)

is depicted. From this figure, it can be seen that transpiration rate in maple, a diffuse-porous species, is substantially higher than in ash, which is ring-porous.

In general, a rise in the transpiration rate was observed during the spring. In conformity with the dye-experiments (Fig. 1), a substantial increase in the transpiration does not occur before the second half of March. After mid-March, a continuous increase in transpiration rate was measured, reaching its highest value at the time when each species leafed out. On the last sampling date (May 7), when both maple and ash had just leafed out, average values of 1.14 g water loss/shoot fr. wt./day and 0.35 g water loss/shoot fr. wt./day were found for maple and ash respectively. Birch however leafed out as early as 31 March and had a value of 0.74 g water loss/shoot fr. wt./day.

#### *Water content of buds in spring*

An increase in weight of buds during spring can be attributed to water influx (increase in fresh weight) as well as to solutes imported with the water (increase in dry weight).

Fresh and dry weight of the buds were determined to provide insight into bud water content during the course of reactivation. This appeared necessary since increase in moisture content at this time can provide a useful indicator for the resurgence of metabolic activity.

Figure 3 shows the results of the analysis with 10 buds of each of the investigated tree species. The fresh- and dry weights of the buds remained relatively constant from the end of January till 23 March, but started rising from there onwards. In maple buds, the dry matter increased rapidly. The mean dry weight of 10 buds was

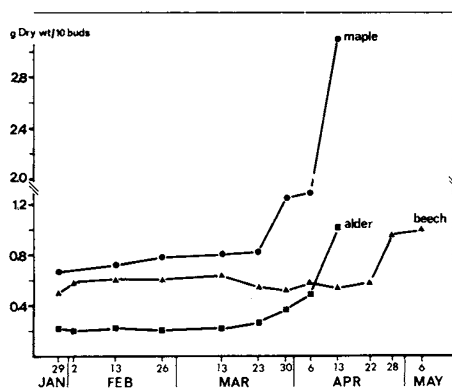


Fig. 3. Increase in dry weight of buds of maple, alder and beech during spring development. Dry weight of 10 buds.

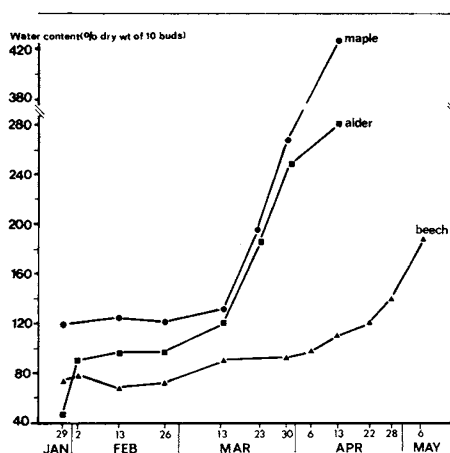


Fig. 4. Increase in water content, expressed as percentage of dry weight of 10 buds in maple, alder and beech.

817 mg on 23 March, but 3144 mg on 14 April. This is an increase of 385% within 22 days. A similar pattern was found for alder. The dry weight increased within three weeks (from 23 March to 13 April) by 427%. Although the bud weight of both species differed greatly, the percentage increase in dry weight during this phase of spring reactivation was almost the same.

Contrarily, dry weight of beech buds remained stable until the end of April, and attained a high value of 138% within a short period of 6 days.

Increase of water content of the buds, which is expressed as percentage of dry weight, is presented in Figure 4. It can be seen that water be-

comes abundant in the buds during spring, even though this occurs at different times among the tree species. The mean water content of 10 maple buds ranges from 117% at the beginning of the investigation (January 29) to 426% on April 13. Alder buds contained only 43% water at the beginning and increased to 282% of the dry weight on April 13. On the other hand, the water content in beech buds increases gradually from 75% at the beginning (January 29) to only 188% on May 6.

#### Changes of cation content in buds

The analytical data of Ca, Mg, and K determinations in buds of maple during spring devel-

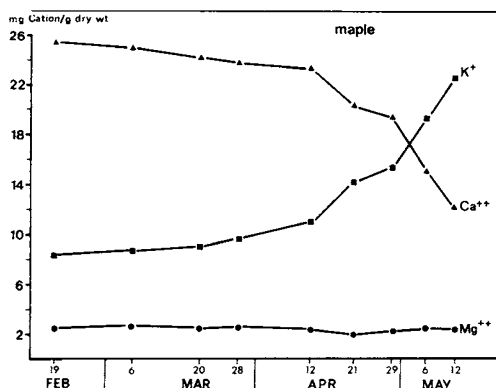


Fig. 5. Changes in cation content (mg/g dry weight) in maple buds during spring.

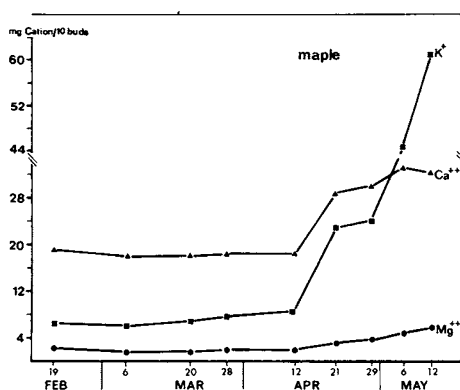


Fig. 6. Changes in cation content (mg/10 buds) in maple buds during spring.

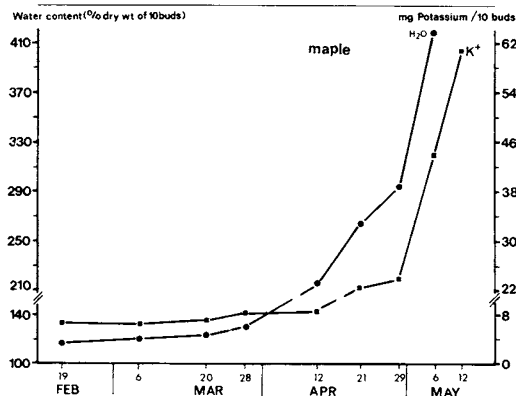


Fig. 7. Comparison between potassium concentration (mg/10 buds) and water content (in percentage of dry weight of 10 buds) in maple buds during spring.

opment are presented in Figures 5 and 6, respectively. The content is expressed for each element in mg/g dry weight. In Figure 6, it is expressed in mg/dry weight of 10 buds. In both presentations, there appears a rising tendency in potassium content. The magnesium concentration remained constantly low. Calcium content started with higher values than potassium and magnesium.

In relation to dry weight of buds, the calcium content decreased substantially at the end of April, but in terms of dry weight of 10 buds, the calcium content remained fairly constant (beech) or rose slightly (maple). Only data for maple are presented here since identical results were found for beech and alder.

#### *Relation between cation concentration and water content in buds*

According to Burström (1948), the uptake of water during bud development is linked to a considerable increase in cation concentration. This statement is confirmed by the present study. However, magnesium remains almost constant or increases insignificantly, while calcium content in contrast to potassium drops early (Figs. 5 & 6). A striking linear relation is shown between potassium accumulation and increase in water content during bud development. This correlation is seen not only in maple (Figs. 7 & 8), but also in beech buds. The correlation coefficient ( $r$ ) is 0,99\*\* for maple and 0.987\* for beech.

Table 1. Periods of sap availability of the examined trees. (Data obtained 0.5 m above ground) and dates from when substantially increase in water uptake was recorded.

Tree species	Spring sap availability			Water uptake
	start (date)	end (date)	duration (days)	(date)
Maple	1 February	9 May	98	31 March
Birch	6 March	3 May	58	23 March
Beech	31 March	3 May	34	7 April
Alder	15 February	12 April	57	
Ash			0	14 April

*Spring sap availability and sap movement in deciduous trees*

In Table 1, a summary of spring sap availability of the examined species is given. The sap was extracted by a puncture method (Essiamah & Eschrich, 1985).

The longest period in which sap could be withdrawn from the cambial region was found in maple. Birch and alder gave an intermediate period while beech gave short periods. Sap could not be withdrawn from ash.

Figure 9 summarises the results of the analytical data of Ca, K, and Mg contents found in spring sap of maple.

Figure 10a–c depicts a model of sap movement in deciduous trees from summer to spring reactivation (May), partly based on the presently and previously published results (Essiamah, 1980, 1982; Essiamah & Eschrich, 1985):

10a): In summer (August), water with dissolved minerals is transported acropetally mainly through the xylem to all parts of the tree. The transpiration stream (open arrow system) thus supplies water for photosynthesis in the leaves. The assimilates, however, are transported from the matured leaves through the phloem (black arrow system) to developing and storage organs and to the developing buds of the next season.

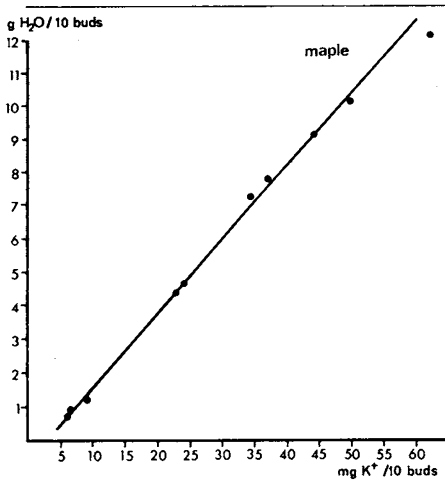


Fig. 8. Correlation between potassium content (mg/10 buds) and water content (g/dry wt. of 10 buds) in maple buds during spring;  $r$ : 0.99;  $P$ : 1%.

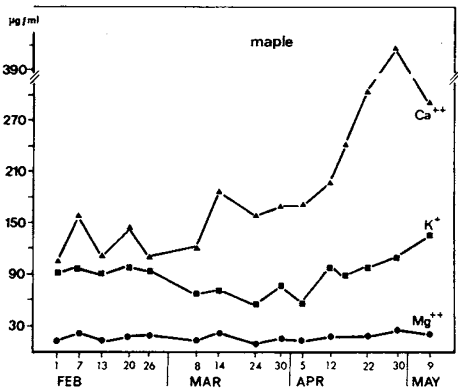


Fig. 9. Changes in cation content ( $\mu\text{g/ml}$ ) in maple spring sap.

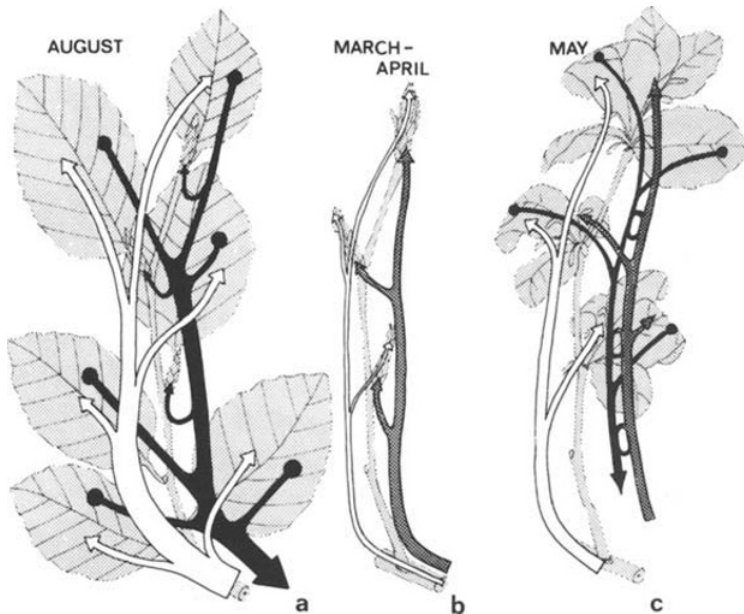


Fig. 10. A model of sap movement in deciduous trees from summer (August) to spring reactivation (May). For explanation see text.

10b): In early spring (March/April), transpiration (open arrow system) is drastically reduced and the stream of assimilates vanishes. The buds, however, swell and increase in weight so that water and solutes must be supplied to them. For this function, the spring sap (dotted arrow system) from the cambial zone serves perhaps as reservoir.

10c): In late spring (May), the transpiration stream increases when the leaves unfold. The leaves at the top begin to export assimilates while regions of shoots with developing buds continue to import organic substances from storage tissues. The spring sap cannot be tapped at this time (after the first week of May) and is probably collected by either the xylem or the phloem depending which tissue is being functional (dotted arrow system). Presumably, the spring sap is finally mixed with the exported phloem sap.

#### Discussion

With the beginning of the growing season in spring, deciduous trees form new conducting elements weeks after the unfolding of leaves (Zimmermann & Brown, 1971). However, be-

fore the new vessels are formed, their buds swell and increase in both fresh and dry weight.

The results of the present study show that a continuous increase of water movement occurs in all five tree species beginning in late March, when buds start developing. This means that water withdrawal from the root area also starts, when buds increase in weight and begin to transpire. This is the beginning of acropetal transport of water and nutrients, as indicated by the increase in potassium concentration in the buds. In this study, potassium concentration rose, and its accumulation correlated with water content/dry weight increase during bud development.

Since the potassium flux in buds is similar to that found in the spring sap (Fig. 9) and since the origin and pathway of the spring sap are still unknown, both the xylem and the phloem may contribute to furnishing the developing buds with nutrients, especially toward the end of spring (Fig. 10c).

For the xylem, one might suggest that nutrients (sugars) enter the vessels and are translocated in axial direction as demonstrated by Sauter et al. (1973) in other diffuse-porous tree species.

Our observations (Essiamah, 1982; Essiamah & Eschrich, 1985) on spring sap indicate that the sap is first formed in the cambial zone of the lower trunk. This activity then extends upward into the upper part of the trunk and later into the twigs and roots. In this sequence, water is initially shifted radially in the stem, which results in the swelling of the cambial tissues, before the sap rises. A direct relationship between spring water uptake and spring sap availability was not observed. The trees were filled with sap (maple at the beginning of February) before a substantial water uptake could be recorded (mid March, Table 1).

Our observation that spring sap is transported along the cambial zone is supported by Höll (1975) who also found that soluble sugars in the cambial zone are present in higher concentrations in spring and might be translocated in part from the older xylem tissues in radial direction via the ray system. An accumulation of these sugars could serve partly as energy source for the resumption of cell division in the cambial zone and partly for attracting water osmotically.

In most of the diffuse-porous trees, acropetal transport of water and nutrients occurs in the vessels of the last years' increments. In ring-porous trees which produce spring sap, like oak, it is largely confined to the very last increment which has been deposited together with the formation of buds. For those ring-porous trees which do not give spring sap (ash), the buds become swollen only after the production of early wood vessels has begun.

Since the upper region of a shoot with its developing buds represent a sink, the phloem could be involved in the supply of nutrients, especially potassium in late spring. Potassium appears in fairly high concentrations in the sieve tube exudate of several species (Ziegler, 1956).

#### Acknowledgements

This research was supported by the German Foundation for International Development to the senior author (S.E.), who also presented it

at the Pan-American Wood Anatomy Meeting held in conjunction with the 36th Annual Meeting of the American Institute of Biological Sciences in Gainesville, Florida, U.S.A., in August 1985.

The manuscript was typed by Mrs. G. Wehr.

#### References

- Burström, H. 1948. The rate of the nutrient transport to swelling buds of trees. *Physiol. Plant.* 1: 124–135.
- Eschrich, W. 1976. Strasburger's kleines Botanisches Praktikum für Anfänger. 17. Aufl. G. Fischer Verlag, Stuttgart, New York.
- Essiamah, S. 1980. Spring sap of trees. *Ber. Deutsch. Bot. Ges.* 93: 257–267.
- 1982. Frühjahrsaktivitäten bei einheimischen Laubbäumen. Thesis. Univ. Göttingen.
- & W. Eschrich. 1985. Changes of starch content in the storage tissues of deciduous trees during winter and spring. *IAWA Bull. n.s.* 6: 97–106.
- Höll, W. 1975. Pattern of sugar concentration and lipase activity in trunks of *Tilia cordata* Mill. from the dormant period to the growing season. *Z. Pflanzenphysiol.* 75: 158–164.
- Huber, B. 1956. Die Transpiration von Sprossachsen und anderen nicht foliosen Organen. *Handb. d. Pflanzenphysiol.* III: 427–435.
- Iwanoff, L. 1924. Über die Transpiration der Holzgewächse im Winter. *Ber. Deutsch. Bot. Ges.* 42: 210–218.
- Pollock, B.M. 1953. The respiration of *Acer* buds in relation to the inception and termination of the winter rest. *Physiol. Plant.* 6: 47–63.
- Sauter, J.J., W. Iten & M.H. Zimmermann. 1973. Studies on the release of sugar into the vessels of sugar maple (*Acer saccharum*). *Canad. J. Bot.* 51: 1–8.
- Ziegler, H. 1956. Untersuchungen über die Leitung und Sekretion der Assimilate. *Planta* 47: 447–500.
- Zimmermann, M.H. & C.L. Brown. 1971. Trees, structure and function. Springer Verlag, Berlin, Heidelberg, New York.