Phyton (Austria)	Vol. 24	Fasc. 1	113—124	15. 2. 1984

Flowering in the *Lemna* System [1])

By

Riklef Kandeler *)

Received June 26, 1983

Key words: Photoperiodism, flower induction, *Lemna*.

Summary

Kandeler R. 1984. Flowering in the *Lemna* system. — Phyton (Austria) 24 (1): 113—124. — English with German summary.

Lemnaceae (duckweeds) are one of the pilot systems to investigate the physiological basis of flowering. Most of the different photoperiodic reaction types are found within these tiny water-plants, which can be held in axenic culture in the laboratory. A short survey on the photo- and chemoregulation of flowering in *Lemnaceae* is given. The significance of photosynthesis for flower initiation, the role of circadian rhythms in photoperiodism and the analysis of the end-of-day far-red effect are discussed in some detail. For a review on all the substances which modify flower initiation in duckweeds following groups has been distinguished: 1. long-day cancellers, 2. long-day supporters, 3. light-on signal cancellers and simulators, 4. end-of-day far-red effectors, 5. flower inhibitors, and 6. flower promotors.

Zusammenfassung

Kandeler R. 1984. Blütenbildung bei *Lemna*. — Phyton (Austria) 24 (1) : 113—124. — Englisch mit deutscher Zusammenfassung.

Lemnaceen (Wasserlinsen) gehören zu den Leitpflanzen bei der Erforschung der physiologischen Grundlagen der Blütenbildung. Fast alle Typen der photoperiodischen Reaktion finden sich unter diesen winzigen Wasserpflanzen, die im Laboratorium in Reinkultur gehalten werden können. Es wird eine kurze Übersicht über die Photo- und Chemoregulation der Blütenbildung gegeben. Eingehender werden die Bedeutung der Photosynthese für die Blütenbildung, die Rolle der circadianen Rhythmik beim Photoperiodis-

---

[1]) Dedicated to Prof. O. H. Volk, Würzburg, on his 80th birthday.

*) Prof. Dr. Riklef Kandeler, Botanisches Institut der Universität für Bodenkultur, A-1180 Wien, Gregor Mendel-Str. 33.

mus und die Analyse des Effekts von Dunkelrot zu Ende der Lichtperiode behandelt. Die die Blütenbildung beeinflussenden Substanzen werden unter den Gesichtspunkten Hemmer bzw. Förderer der Langtagwirkung, Hemmer und Simulatoren des „Licht — an"-Signals, Effektoren der Wirkung von abendlichem Dunkelrot sowie Hemmer und Förderer der Blütenbildung diskutiert.

1. Introduction: Advantages of axenic *Lemna*-culture

Lemnaceae, or duckweeds, are very productive water-plants (Hillman 1961). Frond multiplication proceeds rapidly with a doubling time of fronds — depending on growth conditions — every 1, 2, or at least 4 days (Datko *et al.* 1980). During summer-time lakes and other places with standing water may be covered by a duckweed mat within a few weeks. The plants can be sterilized with mercury chloride and ethanol and than transferred to a liquid medium with a defined mineral salt composition. Such an axenic culture can be supplemented by any water-soluble organic substance to test their effectivity on flower production, for example. Single-plant culture in small test tubes will be possible and after addition of sucrose, amino acids and yeast extract heterotrophic grown pale fronds are developed in continuous darkness. In *Lemna* and *Spirodela* several daughter fronds are produced vegetatively in two pockets of one mother frond, in this way constituting a clone, that is a genetically uniform material.

2. Photoperiodic reaction types in *Lemnaceae*

Today *Lemnaceae* are one of the pilot systems to investigate the physiological basis of flowering. Since 1955, when it was shown that flowering can be induced under controlled conditions in *Lemna gibba* (Kandeler 1955), several working groups in Europe, USA, India and Japan have treated many aspects of flower physiology with this plant material. A short survey on the results obtained until now may be given here.

Recently Landolt (1980) has published the first part of a monographic treatment of *Lemnaceae.* In the determination key he listed 35 taxa within this plant family. In 9 of these species the photoperiodic requirements for flower induction are known. *Lemna gibba, L. minor* and *Spirodela punctata* are long-day plants (Kandeler 1955, Bennink *et al.* 1970, Scharfetter *et al.* 1978); *Lemna perpusilla, L. aequinoctialis* (formerly *L. paucicostata* or *L. perpusilla,* including the strain 6746), *Wolffia microscopica* and *Wolffia brasiliensis* (formerly *W. papulifera*) are short-day plants (Hügel *et al.,* 1979, Hillman 1959, Venkataraman *et al.* 1970, Maheshwari & Seth 1966 a). As Krajnčič (1974) has shown,

Spirodela polyrrhiza is day-neutral and *Wolffia arrhiza* possibly a long-short-day plant (KRAJNČIČ & DEVIDÉ 1980). Consequently, most of the different photoperiodic reaction types are found within the duckweeds and therefore closely related species can be compared for an analysis of day-length effects as in tobacco.

3. Analysis of photoregulation

Photoperiodism is the most popular photoregulation process in flower physiology, but covers only a part of the whole story of light-mediated flower induction. In plants light set in motion several physiological processes simultaneously and — in principle — all of them may have an influence on flower initiation. To disentangle all these photoreactions special light programs and radiation from narrow-band spectral regions has to be used. In addition the very predominant photosynthesis must be held constant or excluded by antimetabolites or by etiolation of the plant material. Many investigations have been made with duckweeds under consideration of these preconditions. Only three components of the whole light effect which have been separated and analysed in more detail, may be reported here.

3.1. Significance of photosynthesis

In accordance with the usual results obtained with other plants high photosynthesis has a flower-promoting effect in the short-day plant *L. aequinoctialis*, strain 6746 (SCHUSTER 1968). High intensity light can compensate the flower-inhibiting effect of long day or a short light break during night in this species. Addition to the nutrient medium of DCMU, a blocker of non-cyclic electron transport in photosynthesis, cancels the effect of high intensity light at concentrations which have only a very low effect on growth rate.

These results, however, are valid only in the case that plants are cultivated in a Hoagland-type medium. POSNER *et al.* (1977) used a modified Hutner medium and than they obtained the opposite results with the same plant material. High intensity light now is inhibiting flower formation under long-day conditions and DCMU re-promotes flowering. A photosynthetic mutant, strain 1073, produced from wild type 6746 by x-irradiation, which has a block between plastochinone and cytochrome f, shows a similar behavior as the DCMU-treated wild type material. Until now, we cannot say which component(s) of the nutrient media may be responsible for reversion of the effect of photosynthesis on flowering. Among other things the modified Hutner medium contains a very high concentration of EDTA (chelating not only the heavy metals but also in part calcium) and a lower calcium concentration.

A further complication comes in, if we include the long-day plant *L. gibba* G1 in our considerations. In this plant DCMU enhances long-day flowering very strongly, and that in diluted Pirson-Seidel medium (KANDELER 1969 a). ATP, which is ineffective in *L. aequinoctialis* under experimental conditions used by POSNER, and also ADP can imitate the effect of DCMU in *L. gibba*. Furthermore arsenate, a phosphorylation uncoupler, inhibits specifically flower initiation in *L. gibba* (KANDELER 1967). It may be that in the long-day plant *L. gibba* a relatively high photophosphorylation is needed for flowering, whereas in the short-day plant *L. aequinoctialis* photosynthesis must work in another way, especially under the conditions of Hutner-medium (GOWER & POSNER 1979).

3.2. The role of circadian rhythms in photoperiodism

Since BÜNNINGS pioneer work it has been well established that daylength measurement by plants and animals uses physiological clocks (BÜNNING 1977). This holds true also for *Lemnaceae*. The late W. S. HILLMAN, one of the best scientists in phytochrome, photoperiodism and *Lemna* physiology, has worked out this in great detail.

During the last 20 years HILLMAN used heterotrophic cultures of the strain 6746 of *L. aequinoctialis* (firstly under the name *L. perpusilla*, than *L. paucicostata*) to exclude the effects of photosynthesis. Instead of regular photoperiods the plant received "skeleton photoperiods", that is a series of 2, 4 or 6 short light pulses equally distributed during the time of photoperiod. With this technique he was able to show characteristic diurnal sensitivity changes to an additional light break (HILLMAN 1976 a, b), which occur in the same manner in green *Lemna* and other plants. Then he demonstrated the influence of photoperiod duration on the time of maximal light sensitivity during dark period. A six-hour increase in length of the light period delays the time of maximal sensitivity by 3,6 hours (measured from the start of each light period).

These results are important, because HILLMAN could show that circadian changes of CO_2 output in *Lemna* are entrained by skeleton photoperiods in the same way. If the plants are cultivated on a nutrient medium with nitrate, the time of maximal CO_2 output depends on the length of daily photoperiod. Also in this case a delay of round-about three hours is caused by a six-hour increase in photoperiod. So it seems to be reasonable to conclude that both rhythms, light sensitivity of flowering and CO_2 flux (that means respiration, in this case) are dependent on the same timer. Nevertheless, both processes can be uncoupled: Replacement of nitrate by aspartate in the medium modifies

the entrainment of CO_2 output but not the photoperiodic control of flowering (at least as estimated by critical daylength).

With green plants of *Lemna gibba G3* Oota and his co-workers have pointed out some metabolic rhythms which all occur under continuous light: CO_2 output, NAD- and NADP-linked glyceraldehyde-3-phosphate dehydrogenases, K^+ uptake, electrolyte efflux and RNA synthesis (Oota & Nakashimà 1978). Therefore, duckweeds may have similar advantages to analyse circadian rhythmicity as *Chenopodium rubrum.*

3.3. The effect of end-of-day far red

Flowering in *L. gibba* can be achieved not only by a long photoperiod or a light break in the middle of the long dark period but also by 10 minutes far-red irradiation at the end of the daily short day. This far-red effect is cancelled, if one minute red is applied to the plants after far red (Kandeler 1962). Some arguments lead to the conclusion that this phytochrome effect is acting in part independently from circadian rhythms and therefore independently from the phytochrome effects in connection with photoperiodism (Hügel *et al.* 1979). On the other hand, end-of-day far red may be an effective part of the light program which is obtained by plants in the natural environment when variably shaded by leaves of other plants. It seems to be plausible that recognition of day length and recognition of leaf shade are strictly separated in plants although the same sensor pigment is used.

During the last fife years we have begun to find out physiological processes which are induced by end-of-day far red in *Lemna.* As an early effect a hyperpolarization of membrane potential can be measured with microelectrode technique in single subepidermal cells (Löppert *et al.* 1978). The hyperpolarization is long lasting and can be reverted by a short red light pulse, if photosynthesis is excluded by DCMU poisoning. After addition of ammonia, which abolishes the active component of membran potential, a phytochrome effect is demonstrable no longer (Kandeler *et al.* 1980). Therefore phytochrome seems to influence the proton gradient at the plasmalemma which is responsible for the active component of membrane potential (Löppert 1979) and delivers the energy for uptake of some organic and anorganic substances into the cell (see co-transport of protons with sucrose, amino acids, nitrate and phosphate: Novacki *et al.* 1978a, b, Ullrich-Eberius *et al.* 1981).

Whether the change of membrane potential is a step between perception of the light signal and the controlled developmental process, that is flower initiation, cannot be said at present. But there are agu-

ments in this direction, which come out from "feeding" experiments whith several substances. These investigations may be summarized in the following section of this paper.

4. Chemoregulation

Many substances, organic and anorganic, has been found to modify the flowering in duckweeds. In all cases which are cited in table 1, the action of these substances is specific in a sense that flowering (and eventually some other developmental processes) but not the general vegetative growth is effected. Six groups of substances has been distinguished as to whether they interact with one of the known light effects or not. Only a few examples may be discussed in some detail.

Table 1

Substances interacting (group 1—4) or not interacting (group 5—6) with certain light effects during flower initiation in *Lemna*

1. Long-day cancellers
Li^+, acetylcholine, eserine
Cu^{++}, ascorbic acid, some amino acids
CCC, ABA
2. Long-day supporters
NAD(P)H, ADP, gibberellin A_3
3. Light-on signal cancellers and simulators
acetylcholine. — valinomycin, gramicidin, cyclic AMP, isoproterenol
4. End-of-day far-red effectors
sucrose, CO_2
5. Flower inhibitors
NH_4^+, optimal conc. of NO_3^-, auxins
6. Flower promotors
EDDHA, salicylic acid, cytokinins

4.1. Substances which cancel the long-day effect

Lithium chloride can be used as an example that addition of a certain substance to the nutrient medium cancels the long day effect. In the long-day plant *Lemna gibba* flowering under long-day conditions is completely inhibited by $3 : 10^{-3}$M LiCl, whereas growth rate is only slightly diminished (Kandeler 1970). That it is especially the long-day effect, which is abolished by lithium, can be seen by comparison with

the behavior of the short-day plant *Lemna aequinoctialis*. If this plant is cultivated under long day lithium has a flower-promoting effect. That meens that also in this case the long-day effect — flower inhibiting in a short-day plant — is cancelled.

Under some circumstances Li^+ acts as an antagonist to K^+ and Ca^{++}, especially if membrane transport processes are involved (see GAILLOCHET 1981, for example). Therefore the interaction of Li^+ with the photoperiodic light effect may be a hint that membrane transport plays a role in the rhythmic phytochrome action and/or the underlying circadian rhythm.

Other mebrane effectors, which are effective in *Lemna* in the same manner as Li^+, are acetylcholine (a transmitter substance which depolarizes the postsynaptic membrane in many animal nerves) and eserine (which inhibits the acetylcholine-degrading enzyme acetylcholine esterase) (KANDELER 1972). Further long-day cancelling substances are Cu^{++} ions (HILLMAN 1962) and ascorbic acid (KANDELER 1971), which both may have to do with the redox state in the plant cells. Some amino acids as aspartate, glutamate, glycin and serin, are effective (NAKASHIMA 1964, TANAKA & TAKIMOTO 1977) and — finally — a change in the internal hormonal balance, especially of gibberellins and abscisic acid (as shown by the effects of CCC, a blocker of gibberellin synthesis, CLELAND & BRIGGS 1969, KANDELER & HÜGEL 1973, and of leaf senescence, KANDELER *et al.* 1974) leads to an abolishment of the long-day effect, too.

4.2. Substances which support the long-day-effect

Substances which support the long-day effect include the central energy-conserving substances (NAD(P)H and ADP (KANDELER 1969, 1970, 1971) and, moreover, gibberellin A_3 (OOTA 1965, GUPTA and MAHESHWARI 1970). For gibberellins it seems to be well established from many investigations on other plants that they are one of the agents which transmit the long-day signal within the plant (KANDELER 1974). The question, why this signal is flower-promoting in long-day plants but flower-inhibiting in short-day plants, can be answered — restricted to *Lemnaceae* — by the hint that the meristem-owned gibberellin production or the ability of meristem for gibberellin retention seems to be different in the two photoperiodic reaction types (HÜGEL 1976a, b). If young flower primordia are explanted and cultured *in vitro* on an agar medium without hormones (except a certain amount of kinetin), than deviations from the normal flower development occur. In the long-day plant *Lemna gibba* a feminization arises: the pistil development is enhanced, whereas the two stamens remain relatively small. The flower development is normalized, if gibberellin A_3 is added to the agar medium. In the short-day plant *L. aequinoctialis*, on the other hand,

a masculinization comes out. At least one stamen is very prominent, but the pistil remains small. In this case CCC, the blocker of gibberellin synthesis, has to be added to the medium for a proper *in vitro* development. Our conclusion is that production or retention of gibberellin in the meristematic tissues may differ in the two plants. Therefore the leaf must deliver a different amount of gibberellin for arriving the right hormone balance at the meristem for flower evocation.

4.3. Substances which abolish or mimic the light-on signal in photoperiodism

In the strain G3 of *Lemna gibba* two long days are needed as a minimal number of inductive photoperiodic cycles. These long days can be inserted in a short-day program to obtain some flowering after one week. Oota (1975) has used this fact to find out the light requiring phases during the first of the two long days (given as continuous light). Irradiation during the first and the twelfth hour of the cycle he found to be very crucial for the flower induction and called them L1- and L2-phase. If, for example, the L1-phase is darkened within the first long day, no flowering takes place. Phytochrome is effective during the L1-phase (Oota 1977). Considering the results of Hillman and others the light requirement during L1-phase may be due to the requirement for the light-on signal to entrain the circadian rhythm. Interestingly enough, Oota (1977a, b) found certain substances, which interact especially with the L1-phase. Addition of acetylcholine to the nutrient medium before or at the beginning of the first long day abolishes the flower-inducing effect of the L1-phase. On the other hand, K^+-ionophores as valinomycin and gramicidin can replace the requirement for L1. Also cyclic AMP and isoproterenol, which activates membrane-bound adenyl cyclase, mimic the L1-phase. In conclusion, some membrane effectors seem to be in a position to interact with the light-on signal of photoperiodism.

4.4. Substances which interact with the effect of end-of-day far red

With regard to vegetative growth of *Lemna* there was stated several times that feeding the plants with sugar can complete or even replace photosynthesis. Also the effect of sucrose and other sugars on flower initiation may be understandable, at least in part, as a complement to the action of photosynthesis. Nevertheless the relation between sugars and flowering is very complex. As we have seen earlier high photosynthesis can overcome or support the flower inhibiting long-day effect in the short-day plant depending on the mineral composition of the nutrient medium. This is true also for sucrose feeding (Posner 1967, Schuster & Kandeler 1970). A further compli-

cation arises if we compare the interaction of sucrose with long day, with a night break of short red light and with end-of-day far red. Under the same conditions, in which sucrose inhibits the long-day effect on flowering in the long-day plant, sucrose enhances the flower-inducing effect of end-of-day far red, and has no effect on the action of red light in the middle of the dark phase (KANDELER 1968). An increase in CO_2 content of the air to 2—5% acts in the same way as sucrose. If the flower-inducing effect of end-of-day far red is relatively low, CO_2 enrichment causes a very distinct improvement of the flower production (KANDELER 1964).

4.5. Substances which inhibit flowering in all photoperiodic reaction types

Now we have to remember that light is not the sole environmental factor which gives the plant some information for the decision to make flowers or not. Temperature, mineral nutrition and other factors are also important. So it may be not surprising to find flower modifying agents which are not intimately connected with photoperiodism and therefore have not contrary but similar effects in long-day and short-day plants. Ammonia, for example, inhibits flower production in *L. gibba* and *L. aequinoctialis* (KANDELER 1969b, HILLMAN and POSNER 1971). The well known fact that optimal nitrogen supply inhibits flowering is true also for duckweeds. ESASHI and co-workers (1972) have summarised their results with a day-neutral, a short-day and a long-day plant in a scheme, from which it can be drawn that the optimal nitrate concentrations for reproductive growth are lower and/or higher then the optimal concentration for vegetative growth. Another group of substances, which belong to the flower inhibitors in *Lemnaceae*, are the auxins (OOTA 1965, GUPTA & MAHESHWARI 1970).

4.6. Substances which promote flowering in all photoperiodic reaction types

MAHESHWARI and co-workers were the first to show the flower-promoting effect of EDDHA (ethylenediamine-di-o-hydroxyphenylacetic acid), which chelates some heavy metals as iron, manganese and copper. At certain concentrations this agent causes a drastic promotion of flowering in *Wolffia microscopica* (MAHESHWARI & SETH 1966), *Lemna aequinoctialis* (MAHESHWARI & GUPTA 1967), *L. gibba* (PIETERSE *et al.* 1970), *L. minor* (BHALLA & SABHARWAL 1972) and *Spirodela punctata* (SCHARFETTER *et al.* 1978). Very similar to EDDHA is the effect of salicylic acid and some related substances (as aspirin). The effectivity of salicylic acid was found by CLELAND, who trieed to discover the flowering hormone by analysing the honeydew from aphid — *Xanthium* inter-

actions and used *Lemna* as a test organism to find out the flower promoting fractions (CLELAND 1974, CLELAND & AJAMI 1974). Salicylic acid cannot overcome the inhibition of a strong non-inductive day length, but it can shift the critical day length (CLELAND & TANAKA 1979). In the long-day plant *L. gibba* the critical day length is shortened roundabout two hours, in the short-day plant *L. aequinoctialis* extended more than one hour. The action mechanism of these interesting substance is unknown until now. A partially but not complete explanation for the effects of EDDHA and salicylic acid may be that they act as manganese chelators. In consequence Mn^{++} is held in solution within the plant and activates IAA oxidase leading in this way to a lowering of the flower-inhibiting auxin level (SCHARFETTER *et al.* 1978).

Cytokinins has been found to promote flowering in the short-day plants *Wolffia microscopica* (MAHESHWARI & VENKATARAMAN 1966) and *L. aeqinoctialis* (GUPTA & MAHESHWARI 1969) under non-inductive conditions culturing the plants in EDDHA- or EDTA-containing media. Also in the long-day plant *L. gibba* benzyladenin causes a further reduction of critical day length if given as a supplement of EDDHA or salicylic acid (PIETERSE & MÜLLER 1977). Higher concentrations of cytokinins, however, inhibit flowering in *L. gibba*. So, as in many other cases, it may be again a certain balance of hormones, which decides on the way of development.

5. Concluding remark

Transformation of a jungle into a cultivated forest needs hard work over a long time. Physiology of flowering may be in a similar situation. Only some aisles or vistas has been worked out so far but the connections between these vistas are lacking in most cases. Without doubt we are far from a coherent and stringent theory for the physiology of induction and evokation of flowering. Nevertheless the advantages and potentials of the *Lemna* system are not exhausted as yet and could be helpful for further investigation and clearing up of the flower physiology of higher plants.

Relief from the Fonds zur Förderung der wissenschaftlichen Forschung in Österreich is gratefully acknowledged.

6. References[1])

BENNINK G. J. H., van den BERG R., KOOL H. J. & STEGWEE D. 1970. Acta Bot. Neerl. 19: 385—392.

[1]) With regard to the extensive reference list, a consequence of the review-like character of the contribution, the redactio exceptionally abandoned the rule (see: Notes for the Contributors, Phyton 20: 199—206, 1980) to quote the cited papers with full titles. The Editors

Bhalla P. R. & Sabharwal P. S. 1972. Acta Bot. Neerl. 21: 200—202.
Bünning E. 1977. Die physiologische Uhr. 3. Aufl. Springer Verlag, Berlin.
Cleland C. F. 1974. Plant Physiol. 54: 899—903.
— & Ajami A. 1974. Plant Physiol. 54: 904—906.
— & Briggs W. S. 1969. Plant Physiol. 44: 503—507.
— & Tanaka O. 1979. Plant Physiol. 64: 421—424.
Datko A. H., Mudd S. H. & Giovanelli J. 1980. Plant Physiol. 65: 906—912.
Esashi Y., Shibasaki T. & Saito K. 1972. Plant Cell Physiol. 13: 623—631.
Gaillochet J. 1981. Planta 151: 544—548.
Gower R. A. & Posner H. B. 1979. Plant Physiol. 63: 548—551.
Gupta S. & Maheshwari S. C. 1969. Plant Cell Physiol. 10: 231—233.
— & Maheshwari S. C. 1970. Plant Cell Physiol. 11: 97—106.
Hillman W. S. 1959. Amer. J. Bot. 46: 466—473.
— 1961. Bot. Rev. 27: 221—287.
— 1962. Amer J. Bot. 49: 892—897.
— 1976 a. Proc. Nat. Acad. Sci. USA 73: 501—504.
— 1976 b. Science 193: 453—458.
— & Posner H. B. 1971. Plant Physiol. 47: 586—587.
Hügel B. 1976 a. Z. Pflanzenphysiol. 77: 395—405.
— 1976 b. Z. Pflanzenphysiol. 80: 283—297.
—, Rottenburg Th. & Kandeler R. 1979. Biochem. Physiol. Pflanzen 174: 761—771.
Kandeler R. 1955. Z. Bot. 43: 61—71.
— 1962. Ber. Dtsch. Bot. Ges. 75: 431—442.
— 1964. Naturwiss. 51: 561—562.
— 1967. European Photobiol. Symp., 19. — 22. IX. 67, Hvar, Jugoslavia, Book of Abstracts, p. 45.
— 1968. Biol. Rundschau 6: 49—57.
— 1969 a. Z. Pflanzenphysiol. 61: 20—28.
— 1969 b. Planta 84: 279—291.
— 1970. Planta 90: 203—207.
— 1971. Z. Pflanzenphysiol. 64: 278—280.
— 1972. Z. Pflanzenphysiol. 67: 86—92.
— 1974. Ber. Deutsch. Bot. Ges. 87: 71—81.
— & Hügel B. 1973. Plant Cell Physiol. 14: 515—520.
—, Hügel B. & Rottenburg Th. 1974. Biochem. Physiol. Pflanzen 165: 331—336.
—, Löppert H., Rottenburg Th. & Scharfetter E. 1980. In: Photoreceptors and Plant Development, Antwerpen University Press, 485—492.
Krajnčič B. 1974. Acta Bot. Croat. 33: 81—88.
— & Devidé Z. 1980. Ber. Geobot. Inst. ETH Stiftung Rübel 47: 75—86.
Landolt E. (Ed.) 1980. Biosystematische Untersuchungen in der Familie der Wasserlinsen (*Lemnaceae*), Vol. 1. Veröff. Geobot. Inst. ETH, Stift. Rübel, Zürich, Heft 70.
Löppert H. G. 1979. Planta 144: 311—315.
—, Kronberger W. & Kandeler R. 1978. Planta 138: 133—136.
Maheshwari S. C. & Gupta S. 1967. Planta 77: 95—98.
— & Seth P. N. 1966 a. Plant Cell Physiol. 7: 163—165.

MAHESHWARI S. C. & SETH P. N. 1966 b. Z. Pflanzenphysiol. 55: 89—91.
— & VENKATARAMAN R. 1966. Planta 70: 304—306.
NAKASHIMA H. 1964. Plant Cell Physiol. 5: 217—225.
NOVACKY A., FISCHER E., ULLRICH-EBERIUS C. I., LÜTTGE U. & ULLRICH W. R. 1978 a. FEBS-letters 88: 264—267.
— ULLRICH-EBERIUS C. I. & LÜTTGE U. 1978 b. Planta 138: 263—270.
OOTA, Y. 1965. Plant Cell Physiol. 6: 547—559.
— 1975. Plant Cell Physiol. 16: 885—894.
— 1977 a. Plant Cell Physiol. 18: 95—105.
— 1977 b. Plant Cell Physiol. 18: 1363—1367.
— & NAKASHIMA H. 1978. Bot. Mag. Tokyo, Special Issue 1: 177—198.
PIETERSE A. H., BHALLA P. R. & SABHARWAL P. S. 1970. Plant Cell Physiol. 11: 675—676.
— & MÜLLER L. J. 1977. Plant Cell Physiol. 18: 45—53.
POSNER H. B. 1967. Plant Cell Physiol. 8: 535—539.
—, POSNER R. S. & GOWER R. A. 1977. Plant Cell Physiol. 18: 1301—1307.
ROTTENBURG Th., SCHARFETTER E. & KANDELER R. 1981. Photosynthesis Research 1: 251—258.
SCHARFETTER E., ROTTENBURG Th. & KANDELER R. 1978. Z. Pflanzenphysiol. 87: 445—454.
—, BÄCK E. & KANDELER R. 1981. Poster at the Europaean Symposium "Light Mediated Plant Development", Bischofsmais, Germany, 1981.
SCHUSTER M. 1968. Thesis, Univ. Würzburg.
— & KANDELER R. 1970. Z. Pflanzenphysiol. 63: 308—315.
TANAKA O. & TAKIMOTO A. 1977. Plant Cell Physiol. 18: 27—34.
ULLRICH-EBERIUS C. I., NOVACKY A., FISCHER E. & LÜTTGE U. 1981. Plant Physiol. 67: 797—801.
VENKATARAMAN R., SETH P. N. & MAHESHWARI S. C. 1970. Z. Pflanzenphysiol. 62: 316—327.