

## Photosynthesis of sun and shade leaves of field-grown grapevine (*Vitis vinifera* L.) in relation to leaf age. Suitability of the plastochron concept for the expression of physiological age

by

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**Summary:** The relationship of photosynthesis to leaf age for sun and shade leaves was investigated in a field experiment over two years. The objective was to test the suitability of the plastochron index concept, proposed by ERICKSON and MICHELINI (1957), for the description of age-related changes in leaf photosynthetic activity in the field. The duration of a plastochron decreased strongly and similarly for sun and shade shoots with increasing temperature, whether temperature was expressed as a daily heat sum (degree days  $> 10^{\circ}\text{C} \cdot \text{dd}^{-1}$ ) or as the mean of daily minima and maxima. The responsiveness to temperature decreased during the season and the lower threshold for development increased. Plastochron duration was insensitive to the amount of light received in the canopy. Expressing time elapsed between leaf unfolding and attaining maximum rates of photosynthesis in degree days or days yielded changing relationships depending on when during the season leaves unfolded. In contrast, this relationship was constant if time was expressed in plastochrons. The results show that the plastochron is an adequate indicator of time as the plant experiences it, and is superior to the thermal time (degree day) and chronological time expressions commonly used to relate photosynthesis to development.

**Key words:** photosynthesis, sun and shade leaves, leaf age, plastochron index, leaf plastochron index, plastochron duration, thermal time.

### Introduction

Many features of leaf structure and physiology vary with leaf age. Among these are important changes in photosynthetic activity and stomatal conductance (FIELD 1987). Most of the studies on photosynthesis and leaf age, including several on *Vitis vinifera* L. (KRIEDEMANN *et al.* 1970; ALLEWELDT *et al.* 1982), have been conducted in controlled environments in order to single out leaf age as independent variable and avoid complications through effects of fluctuating temperature and light intensity on photosynthesis as the dependent variable. Only under these sets of constant conditions can leaf age be expressed on the basis of chronological time in days or months and it is generally accepted that grape leaves reach their maximum photosynthetic activity after about 30-40 d with a gradual decline thereafter (KRIEDEMANN *et al.* 1970; INTRIERI *et al.* 1992). However, any functional relationship between leaf age and photosynthesis obtained in these studies will be specific to the particular set of conditions present, since the rates of development and ageing will be dependent on several environmental factors, especially temperature (MONTEITH 1979). As such, extrapolation to different climates or environments with different temperature and light regimes, or even to constantly changing conditions as in field situations, is difficult if not impossible.

This has long been recognized in models of plant growth, where a thermal time or heat unit system is frequently used as a more suitable basis for the expression of time as the plant experiences it (BAKER *et al.* 1981; GUTIERREZ *et al.* 1985). Consequently, any suitable description

of physiological age has to be a plant feature which can serve as an integrator of the environment. Of interest here is the plastochron, originally termed *Formungszeit* by ASKENASY (1880), or the unit of time corresponding to the interval between two successive similar, periodically repeated events. ERICKSON and MICHELINI (1957) used ASKENASY's concept in proposing developmental indices for shoot growth and leaf ageing, the plastochron index (PI) and the leaf plastochron index (LPI). In the original formulation of the PI, leaves on a primary shoot are identified with successive integers  $n = 1, 2, \dots$ , in order of their appearance, and the age of the plant is roughly designated by the number of leaves which have appeared,  $n$ . Since one leaf appears each plastochron, a plant with  $n$  leaves can also be said to be roughly  $n$  plastochrons old. The PI assumes that homologous organs such as leaves, at successive nodes, grow exponentially at equal relative growth rates, and thus the plastochron remains constant under a given set of conditions. However, for many plants, including grapevines, these requirements are not met (HILL and LORD 1990) in that decreasing rates of leaf appearance during the season cause plastochrons to vary with time (SCHULTZ 1992).

Additionally, in a field situation, an individual plant is an aggregate of leaf populations of multiple ages distributed through an array of microsites mainly differing in light climate. Thus, any suitable physiological index for the description of age has to be largely insensitive to light intensity, and thus stable over a wide range of photosynthetic supply values caused by differences in light exposure.

The objectives of the present paper were (1) to demonstrate the suitability of the plastochron and leaf plastochron indices for the description of physiological age throughout the lifespan of grapevine sun and shade shoots or leaves in a field situation, (2) to show how the plastochron responds to the environmental factors temperature and light and how the plastochron concept can be used to describe age related processes such as changes in photosynthetic activity, (3) to outline the advantages of physiological over chronological time expressions.

### Material and methods

**Plant material and experimental site:** Experiments were conducted over two years (1987-1988) on 9-year-old field-grown White Riesling grapevines (*Vitis vinifera* L.) clone 198 Gm on 5 C rootstock at the State Research Institute in Geisenheim, Germany (50° North, 8° East). Details of growing conditions and soil analyses are given elsewhere (SCHULTZ 1990). Vines were dormant pruned to 10 buds/m<sup>2</sup> in January. Vineyard management was according to commercial practices with the exception that shoots remained unhedged (no removal of the apical shoot portion).

**Definition of sun and shade shoots:** Sun shoots were defined as shoots growing on the canopy exterior well exposed to light throughout most of the day. Shade shoots grew in the canopy interior receiving less than 12 mol photons · m<sup>-2</sup> · d<sup>-1</sup> (PFD) integrated over a photoperiod. By definition, shade shoots were present only after canopy closure, about one week before full bloom.

**Phenology:** The timing of crop development was described using thermal time (TT) or accumulated heat units expressed in degree days (°C d) (WINKLER and WILLIAMS 1939). Heat unit accumulation started at phenological stage 05 (first leaf approx. 20 mm long) of the EICHORN and LORENZ (1977) development scale. Thermal time was calculated from daily maximum and minimum temperatures assuming a lower threshold temperature (base temperature) of 10 °C (WINKLER and WILLIAMS 1939; GUTIERREZ *et al.* 1985). Temperature data were obtained from the Agricultural Meteorology Experiment Station, National German Weather Service, Geisenheim, located about 1500 m from the experimental site.

**Determination of physiological age:** Leaf age was expressed in plastochrons and the plastochron index (PI) was used to define leaf position on a shoot, using ERICKSON and

MICHELINI's (1957) equation:

$$PI = n + \frac{\ln L_n - \ln(30)}{\ln L_n - \ln L_{n+1}} \quad (1)$$

where  $n$  is the number of leaves larger than the reference length of 30 mm (lamina length) in basipetal direction and  $L_n$  and  $L_{n+1}$  are the lengths of leaves just longer and shorter than the reference length. The leaf plastochron index (LPI) (ERICKSON and MICHELINI 1957) was used to express the developmental age of single leaves on a shoot in plastochrons:

$$LPI = PI - i \quad (2)$$

where  $i$  is the number of nodes basipetal to the leaf position of interest. The time needed to complete one plastochron was termed plastochron duration, PD (d). The temperature dependence of PD was described with an exponential equation:

$$PD = PD(\max) \cdot e^{-(k \cdot TT)} + PD(\min) \quad (3)$$

where PD is expressed in d and PD(max) and PD(min) are the maximum and minimum plastochron durations, respectively. The TT denotes the thermal time per d ( $^{\circ}\text{C} \cdot \text{d}^{-1}$ ), and  $k$  is a temperature coefficient. In an alternative formulation of the model in eq. 3, TT was replaced by mean daily temperature (MDT,  $^{\circ}\text{C}$ ), thus not considering a lower temperature threshold for growth. Both versions of the model were fitted to data on the development of 5-10 sun and shade shoots, whose PI and LPI was recorded at 1-3 d intervals from bud break to harvest in 1988. Fitting was done using the least square non-linear regression procedure PROC NLIN of SAS (SAS Institute 1987).

**Light measurements:** Measurements of PFD on the canopy exterior and interior were conducted with 6-8 quantum sensors (Li-Cor Inc., Lincoln, Nebraska, USA) mounted on metal rods placed near individual upright-growing shoots at similar angles and azimuths as most of the leaves on these shoots. A data logger (Li-Cor Inc.) was used to record data in 1 min intervals. Measurement periods were 7-15 d on 5 occasions during the season (June-September in 1987 and 1988). The PIs and LPIs of the experimental shoots were measured every morning.

**Gas exchange measurements:** As previously described in detail (SCHULTZ 1991), net  $\text{CO}_2$  assimilation rate ( $A$ ) was measured throughout the growing season (20 occasions in 1987, 46 occasions in 1988) with a transportable, open-system gas exchange apparatus (Walz, Effeltrich, Germany) (SCHULZE *et al.* 1982).

Measurements were conducted between 9 a.m. and 12 a.m. on days when conditions were optimal for high rates of photosynthesis ( $\text{PFD} > 1400 \mu\text{mol} \cdot \text{m}^{-2} \cdot \text{s}^{-1}$ , optimum leaf temperature and non-limiting air vapour pressure deficits (SCHULTZ 1990)). Ten shoots/vine on 10 vines were selected after bud break or at canopy closure (shade shoots) and measurements were conducted on these shoots throughout the season. For measurements on shade leaves, shoots growing inside the canopy were temporarily exposed to full sun light. No photoinhibition was observed under these conditions. Boundary layer conductance of leaves was estimated according to GATES (1980). All gas exchange parameters were calculated using the equations of VON CAEMMERER and FARQUHAR (1981).

## Results and discussion

**Temperature response:** The velocity of leaf appearance and leaf development, i.e. the plastochron duration (PD), was strongly and similarly related to both temperature parameters for sun and shade shoots (*cf.* Fig. 1 A, B, C and insets). Near the lower temperature

threshold for growth ( $TT = 0$ ,  $MDT = 10\text{ }^{\circ}\text{C}$ ), PD decreased exponentially, asymptotically approaching a minimum value (maximum velocity of development) at about  $8\text{ }^{\circ}\text{C d}^{-1}$  TT or approximately  $17\text{ }^{\circ}\text{C MDT}$  (Fig. 1). An upper temperature threshold for development was not reached under the given climatic conditions and earlier investigations suggest such a threshold, if present, would be above  $30\text{ }^{\circ}\text{C MDT}$  (BUTTROSE 1969). The lower temperature threshold for growth was found to be close to the commonly accepted  $10\text{ }^{\circ}\text{C MDT}$  (or  $0\text{ }^{\circ}\text{C d}^{-1}$  TT) for grapevines (WINKLER and WILLIAMS 1939; GUTIERREZ *et al.* 1985) during the phase of rapid shoot growth in the early part of the season (Fig. 1 A, inset). However, the responsiveness of development to temperature decreased during the season resulting in an increasing base temperature and longer PDs at optimal temperatures (Fig. 1 B, C and insets). For example, in the period  $TT\ 670-980$  (August-September), the completion of a plastochron at a  $TT$  of 4 and  $12\text{ }^{\circ}\text{C d}^{-1}$  ( $13$  and  $20\text{ }^{\circ}\text{C MDT}$ ) required 14 and 4 d, respectively (Fig. 1 C and inset) as compared to only 6 and 2 d in the period  $TT\ 100-240$  (May-June) (Fig. 1 A and inset).

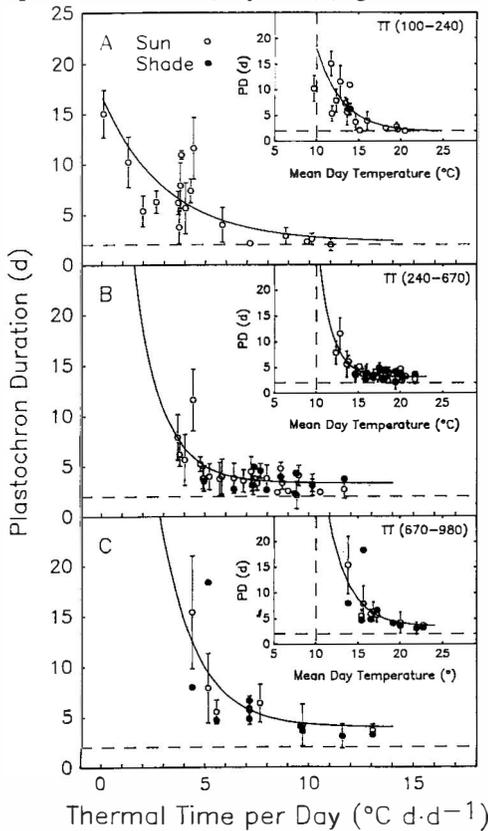


Fig. 1: Plastochron duration of sun and shade shoots in relation to two temperature parameters, thermal time per day (A, B, C) and mean day temperature, MDT (A, B, C insets), during three periods of the growing season in 1988. Numbers in parenthesis in the insets indicate length of measurement periods expressed in thermal time (TT,  $^{\circ}\text{C d}$ ). Data are mean values  $\pm$  SE of 5-10 shoots. Continuous lines represent model estimates based on non-linear regression analyses of eq. 3. Horizontal and vertical dashed lines represent a plastochron duration of 2 d and a lower temperature threshold of  $10\text{ }^{\circ}\text{C}$ , respectively. Note that TT (100-240), (A), represents phenological stage prior to canopy closure, where no shade shoots are present. Estimated model parameter for TT as dependent variable were (A):  $PD(\text{max}) = 14.4$ ,  $PD(\text{min}) = 2.2$ ,  $k = 0.33$  ( $R^2 = 0.91$ ); (B):  $PD(\text{max}) = 65.7$ ,  $PD(\text{min}) = 3.3$ ,  $k = 0.74$  ( $R^2 = 0.95$ ); (C):  $PD(\text{max}) = 107.6$ ,  $PD(\text{min}) = 4.0$ ,  $k = 0.58$ , ( $R^2 = 0.87$ ); and for MDT (A, inset):  $PD(\text{max}) = 415.8$ ,  $PD(\text{min}) = 1.8$ ,  $k = 0.33$  ( $R^2 = 0.88$ ); (B, inset):  $PD(\text{max}) = 15350.9$ ,  $PD(\text{min}) = 3.2$ ,  $k = 0.63$  ( $R^2 = 0.95$ ); (C, inset):  $PD(\text{max}) = 2104.4$ ,  $PD(\text{min}) 3.4$ ,  $k = 0.39$  ( $R^2 = 0.83$ ).

These data indicate that the basic postulate of ERICKSON and MICHELINI (1957) of a constant relationship between PI or LPI and temperature is not met. Nevertheless, the PI concept is still applicable and can be particularly useful for modelling of phenology (HODGES and RITCHIE 1991), if the change in heat unit requirement for the formation of a plastochron for any particular stage of plant development is known (CAO and MOSS 1989). This approach has recently been used to model shoot growth and leaf area formation of several grapevine canopy systems (SCHULTZ 1992) and the limitations of grape leaf photosynthesis during ageing (SCHULTZ 1994).

**Light response:** The plastochron-duration was independent of the amount of light received by shoots located in different canopy zones (Fig. 2) at all times during the season (data not shown), suggesting that the plastochron is largely independent of photosynthetic supply. Similar results were obtained with grapevines grown in controlled environments (BUTTROSE 1969), but the PD in other species can respond to increases in daily light integral and maximum light intensity (SNYDER and BUNCE 1983). The remarkable consistency in the rate of leaf appearance of sun and shade shoots occurs despite 3- to 4-fold differences in dry weight (BUTTROSE 1968; SCHULTZ 1990). This is important in applying the plastochron concept to whole grapevine canopies where shoots can grow in vastly different light micro-climates.

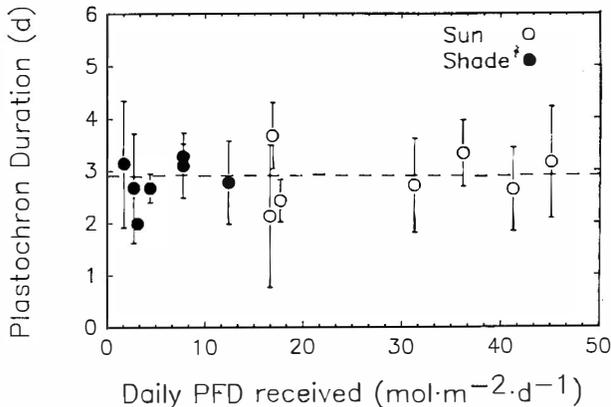


Fig. 2: Relationship between plastochron duration of sun and shade shoots and daily received light integral at different locations within a canopy. Data were collected on successive days in July (TT 8-12 °C·d<sup>-1</sup>, MDT 17-20 °C). Total length of measurement period was 17 d (July 5-21, 1988; TT 427-544). Data are mean values  $\pm$  SE from 6-8 shoots.

**Relation to photosynthesis:** Measurements of sun leaf photosynthetic activity in 1987 and 1988 showed that, based on chronological time, similar maximum photosynthetic rates,  $A_{max}$ , were reached about 15-20 d later in 1987 than in 1988, although bud break and thus unfolding of the investigated leaves occurred about 3-5 d earlier in 1987 (Fig. 3 A). Expressing age in TT (starting at bud break) or plastochrons (LPI) eliminated differences in the chronological time required to reach  $A_{max}$  between years (Fig. 3 B, C).

Since the temperature requirement for the completion of a plastochron increased during the season (cf. Fig. 1 A, B, C), the question arose whether the relationship between photosynthetic activity and LPI would also change. To test this, A and LPI of developing leaves unfolding at different times during the season were measured until maturity (reaching of  $A_{max}$ ). Additionally, chronological time and thermal time elapsed between date of unfolding and date of measurements of A were also recorded.

Shade leaves older than LPI 5 had reduced photosynthetic rates as compared to sun leaves (Fig. 4), but the basic relationship of A to LPI (indicated by the slope of the lines) stayed constant throughout the season for both sun and shade leaves, deteriorating slightly only very late in the season close to fruit harvest (TT > 1000 = mid-October). In contrast, the TT and chronological

time required for a leaf to reach a certain level of photosynthetic activity increased substantially in the later phases (after 670 TT) of the growing season (Fig. 4 K, L, N, O), reflecting slowed development and metabolism. Plotting A vs. chronological time also showed considerable scatter in the early part of the season (Fig. 4 C, TT 140-240), where, depending on the prevailing temperature after a leaf has unfolded, the time required to reach  $A_{\max}$  was between 15 and > 42 d (Fig. 4 C).

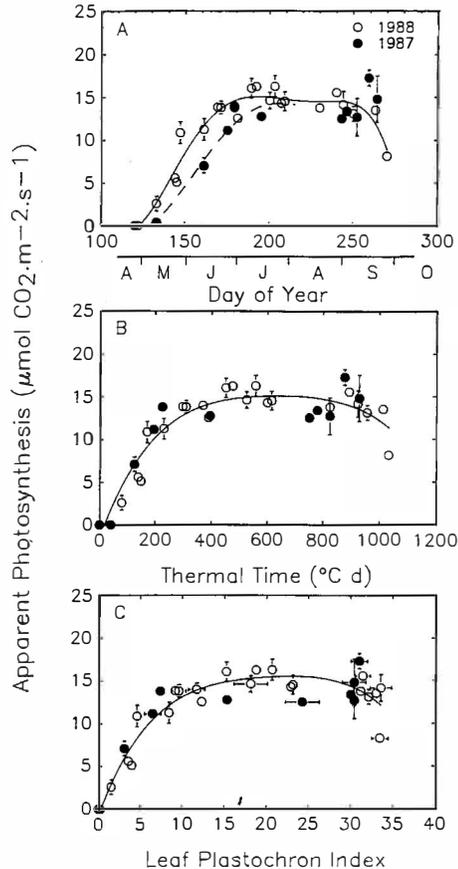


Fig. 3: Development of maximum photosynthetic activity of sun leaves during the growing seasons 1987 and 1988. (A) in relation to the day of year; (B) in relation to thermal time starting at bud break; (C) in relation to the leaf plastochron index. Measurements were conducted under optimal conditions and data represent averages  $\pm$  SE of 5-10 leaves.

The data suggest that shoot and leaf development, reflected in the LPI, are tightly coupled to the development of the photosynthetic apparatus. Thus, although the first and last leaf studied emerged more than 100 d apart and differed 4-5 fold in final leaf area, all leaves followed a similar physiological time course. A similar coupling of photosynthetic history to physiological time has been observed with tobacco (RAWSON and HACKETT 1974). Although the difference between the various expressions of time may be smaller in regions with a more uniform climate, they nevertheless should be considered when referring to studies conducted under field conditions and where age was expressed as chronological time (VASSILIEVA 1956; MOTORINA 1958; STOEV *et al.* 1966; KRIEDEMANN 1968; SVIHRA 1976; SCHOLEFIELD *et al.* 1978; HUNTER and VISSER 1988).

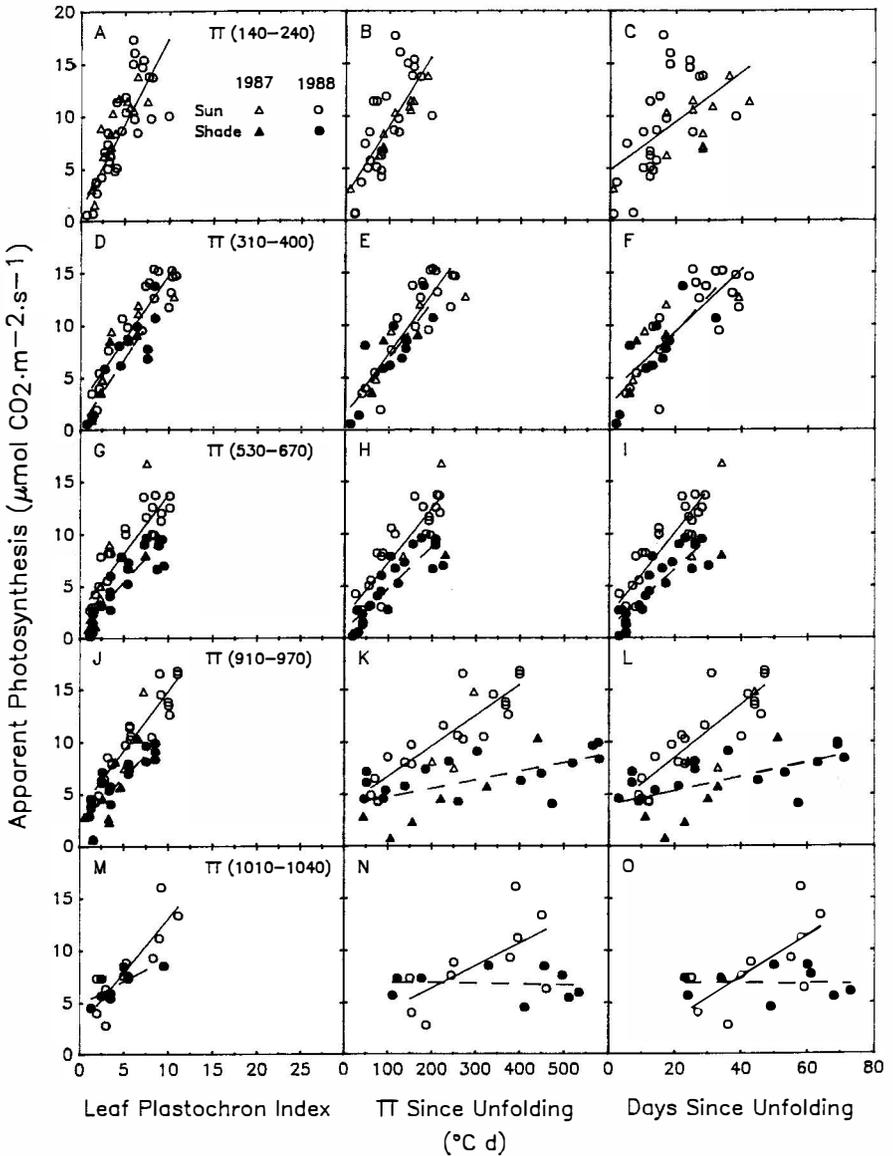


Fig. 4: Photosynthetic activity of sun and shade leaves between leaf unfolding and maturity (reaching of maximum photosynthetic rates) in relation to the leaf plastochron index (A, D, G, J, M), thermal time since unfolding (B, E, H, K, N), and days since unfolding (C, F, I, L, O), for leaves appearing at different times during the 1987 and 1988 seasons. Lengths of measurement periods are given as thermal time, TT, in parenthesis for each row of figures. Linear regression lines are shown for clarity.

Provided that the growing conditions are known, and assuming that the relationship of PD to temperature is roughly the same for different varieties and climates, it should be possible to convert data on the relationship between A and age (as chronological time) for grapevines obtained from the literature to a general A vs. LPI relationship. Fig. 5 shows recalculated data from the literature in comparison to the relationship reported in Fig. 3 C. Data are expressed

in % of  $A_{\max}$  because photosynthetic rates in the cited studies varied. Also, studies were selected where actively growing shoots were investigated to minimize possible differences in the PD vs. temperature relationship in response to time during the season (see also Fig. 1). Since growth conditions with respect to temperature were not specifically outlined in KRIEDEMANN *et al.* (1970) but termed optimal, a plastochron duration of 2.2 d, as found optimal for White Riesling in the present study, was assumed. Also, leaf unfolding in KRIEDEMANN *et al.* (1970) was designated a LPI of -1, based on observations on the variety Thompson Seedless.

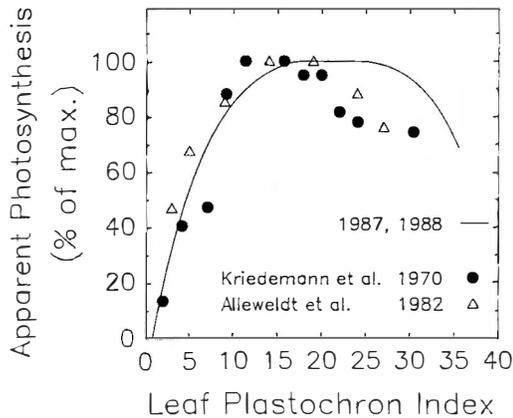


Fig. 5: Relationship of apparent photosynthesis (in % of maximum) to leaf plastochron index (continuous line) as shown in Fig. 3 in comparison to recalculated relationships obtained from various publications.

Using the plastochron concept, a common relationship between physiological age and maximum photosynthetic activity is obtained, at least until  $A_{\max}$  is reached (Fig. 5). However, subtle differences in minimum PDs for different varieties can be expected, since the intrinsic rate of development is variety-dependent (McINTYRE *et al.* 1982). The differences in the rate of decline in photosynthetic activity after  $A_{\max}$  was reached between the present study and those used in the comparison (Fig. 5) may be related to differences in root volume between field and potted plants and the associated differences in hormone levels interacting with stomatal and photosynthetic functioning (BLACKMAN and DAVIES 1984).

For grapevines, the plastochron concept proved to be a better time basis for the description of age-related photosynthetic activity than chronological time or thermal time, since it is independent of leaf expansion at different times of the season but reflects the progress in plant development.

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