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Seasonal growth and nitrogen distribution in grapevine leaves, shoots and grapes

by

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Jahresverlauf des Wachstums und der Stickstoffverteilung in Blatt, Trieb und Traube von Weinreben

Zusammenfassung: In einem Ertragsrebbberg wurden in regelmäßigen Abständen während des Jahres Proben von Blättern, Trieben und Trauben genommen. Davon wurden das Frisch- und Trockengewicht, die Blattfläche sowie der Wasser- und Stickstoffgehalt bestimmt. Das Wachstum wurde auf der Basis von Grad-Tagen $> 10^{\circ}\text{C}$ (GT) dargestellt. Das Primärblatt-Wachstum konnte in zwei Phasen unterteilt werden. Die erste Phase dauerte bis zum Alter von 250 GT und war durch ein rasches Blattwachstum gekennzeichnet ($0.0043\text{ g} \cdot \text{GT}^{-1}$). Die zweite Phase wies nur eine geringe Wachstumsrate von $0.0006\text{ g} \cdot \text{GT}^{-1}$ auf und dauerte bis zum Blattfall. Bei 250 GT war das Blatt voll entfaltet und die N-Einlagerung abgeschlossen. Die spezifische Blattfläche ($\text{m}^2 \cdot \text{g}^{-1}$) fiel nach einem kurzen Anstieg mit zunehmendem Blattalter kontinuierlich ab. N- und Wasser-Gehalte nahmen im Verlaufe des Jahres ebenfalls ab. Im Spätsommer sind zwar mehr Geizblätter als Primärblätter vorhanden, die gesamte Blattfläche und -masse sowie die absolute N-Menge waren jedoch ungefähr gleich auf Haupt- und Geiztriebe verteilt. Die relative Verteilung von Trockensubstanz (TS) in Blättern und Trieben unterschied sich von der N-Verteilung. Der größte Anteil an TS war in den Trieben lokalisiert, während sich in den Blättern die größte N-Menge vorfand.

Key words: growth, leaf, shoot, bunch, dry matter, nitrogen, growing season, temperature, heat sum.

Introduction

Most data on the number, dry mass, water and nitrogen content of vegetative and of reproductive organs of grapevines reported in the literature were collected at harvest, while less work has been done on the development of yield formation and the build-up of the vegetative structures during the growing season. Often these data are given in terms of fresh weight of plant parts; the allocation of photosynthates, however, is more accurately expressed on a dry weight basis. In addition, only sparse information exists on growth rates of individual leaves, shoots or grapes, on the area/weight relationship of leaves and on the distribution of nitrogen in leaves, shoots and grapes during their development. This kind of data was needed for the construction of a grapevine model which has been developed recently (WERMELINGER *et al.* 1991). On the one hand some parameters for the model's needs were missing in the literature, and on the other hand it is only possible to a limited extent to use data from the literature for local situations.

Materials and methods

A vineyard of 18-year-old grapevines (*Vitis vinifera* L.) of the variety Blauburgunder (Pinot noir) clone Mariafeld on a 5 C rootstock located at the Federal Research Sta-

tion FAW in Wädenswil, Switzerland was used for growth analysis in 1988. The plants were grown at a spacing of 2.2 m × 1.1 m, double cane pruned and received no fertilizers in that year. Summer pruning and canopy management was done as follows: extra shoot removal, suckering and topping of inter-row shoots in late May (approx. 25 % loss), hedging of the topmost shoot parts and removal of basal lateral shoots in mid July (approx. 25 % loss) and a second topping in late August (approx. 10 % loss). An average number of 14 shoots/vine was retained. The vines were cultivated according to local practices. Final grape harvest occurred on October 17. From budbreak (April 21) to the end of leaf fall (mid November) entire shoots were sampled (including lateral shoots) at intervals of approx. 1 week until mid June and of about 3–5 weeks later on. Per sampling date 2 shoots of 3 plants (totalling 6 shoots) were harvested, sampling the same plant only once. The shoots were transferred in plastic bags to the laboratory, where shoot length, fresh and dry weight of shoots and leaves of both primary and lateral shoots were recorded, as well as number and weight of grape clusters and berries. Leaves of the primary shoots were treated individually according to their age (position on the shoot), whereas lateral leaves were pooled. Leaf and cluster petioles as well as the tendrils were weighed with the shoot. From these data water content (% fresh weight) and specific leaf area (SLA, area per weight as $\text{m}^2 \cdot \text{g}^{-1}$) were computed. The material was dried at 105 °C for 1 h and subsequently at 60 °C for 2 d, ripe grapes for several days. For determination of the nitrogen content the 6 replicates of selected plant parts were pooled and analyzed for total N by means of an NCS autoanalyzer (Carlo-Erba) with thermal conductivity detection.

Physiological time expressed as degree-days (dd), i.e. the integral of daily temperatures above the developmental threshold of 10 °C (WINKLER *et al.* 1974; GUTIERREZ *et al.* 1985), was calculated, using the sine integration through the daily maximum and minimum temperatures (FRAZER and GILBERT 1976; cf. WILSON and BARNETT 1983). Weather data were obtained from the automatic weather recording station at Wädenswil of the Swiss Meteorological Institute.

Results

All data are presented on a degree-day basis. For reasons of better comprehension, a calendar scale has been added where the abscissa indicates the seasonal time and not organ age. The seasonal time represented by the accumulated heat above 10 °C starts on January 1 with budbreak occurring at 35.8 dd (April 21), while the age of individual leaves is expressed as dd after leaf birth. The year 1988 experienced a somewhat higher dd sum (1155.3 dd) than the preceding 3 years' average (1121 ± 5.4 dd). The difference was realized mainly in spring and early summer, while the remainder of the year was comparable with earlier years. In absolute terms, July and August received most dd (262, 263 dd, respectively). Blooming was at 335 dd (June 19) and final grape harvest at 1135 dd (October 17).

Leaf growth

The area and dry mass growth rates of leaves of the primary shoots (henceforth called primary leaves), depending on their individual age (not time of the year!), are depicted in Fig. 1, while the formation rates of primary and lateral leaves can be extracted from Fig. 4 A. Most primary leaves (leaves no. 1–15, the basal leaf being no. 1) reached about the same final leaf area of approx. 200 cm^2 (Fig. 1 A) and a final dry weight of roughly 1.5 g (Fig. 1 B). Fresh weight followed the same pattern reaching a plateau at approx. 4–5 g. The growth rate of expanding leaves (younger than 250 dd)

was $0.0043 \text{ g} \cdot \text{dd}^{-1}$, followed by a lower rate of $0.0006 \text{ g} \cdot \text{dd}^{-1}$. The first and hence oldest two leaves (indicated by numbers 1 and 2 in Fig. 1) emerging simultaneously from the buds stayed smaller than the subsequently formed ones. The later developing leaves reached a greater weight and size. Leaves younger than no. 15 were not included in these figures, because at the stage of approx. 21 leaves/shoot the vines were pruned back to approx. leaf no. 16 (hedging).

The relationship between leaf area and dry weight (specific leaf area) is shown in Fig. 2 A. After a rapid increase of leaf area rather than weights, in young leaves a peak average of $0.022 \text{ m}^2 \cdot \text{g}^{-1}$ ($45.5 \text{ g} \cdot \text{m}^{-2}$ in other terms) was reached at about 150 dd, followed by a gradual decrease until leaf abscission. This means that the aging leaves

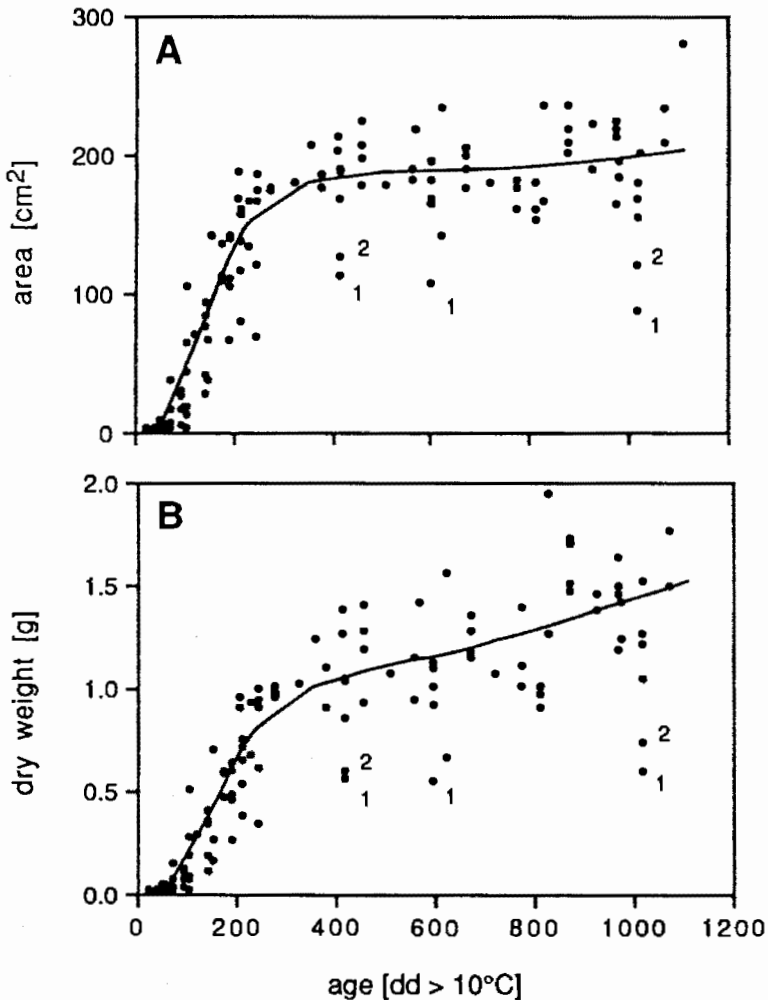


Fig. 1: Development of leaf area (A) and dry weight (B) of primary grapevine leaves depending on their individual age. Numbers 1 and 2 indicate leaf position. — Regressions: Lowess smoother (CLEVELAND 1985); leaves 1 and 2 omitted.

Flächen- (A) und Trockengewichtszunahme (B) von Primärblättern bei Weinreben in Abhängigkeit von ihrem individuellen Alter. Die Zahlen 1 und 2 bezeichnen die Blattposition.

became heavier relative to their size. Senescent leaves approached a weight per area almost twice the one at the age of maximum SLA. Water content (Fig. 2 B) was age dependent and decreased steadily as the leaves grew older, the decrease being most pronounced in young and in senescent leaves. In newly formed leaves it was nearly 80 % and it fell below 70 % in aging leaves. The water content of the pooled lateral leaves was comparable to that of primary leaves, but decreased less markedly during the season (Fig. 6 A), due to the pooling of all lateral leaves. The longevity of the first primary leaves averaged approx. 900 dd (120 d).

The N content of the primary leaves showed a clear pattern with increasing leaf age (Fig. 3 A). Very young leaves had an extremely high N concentration of more than

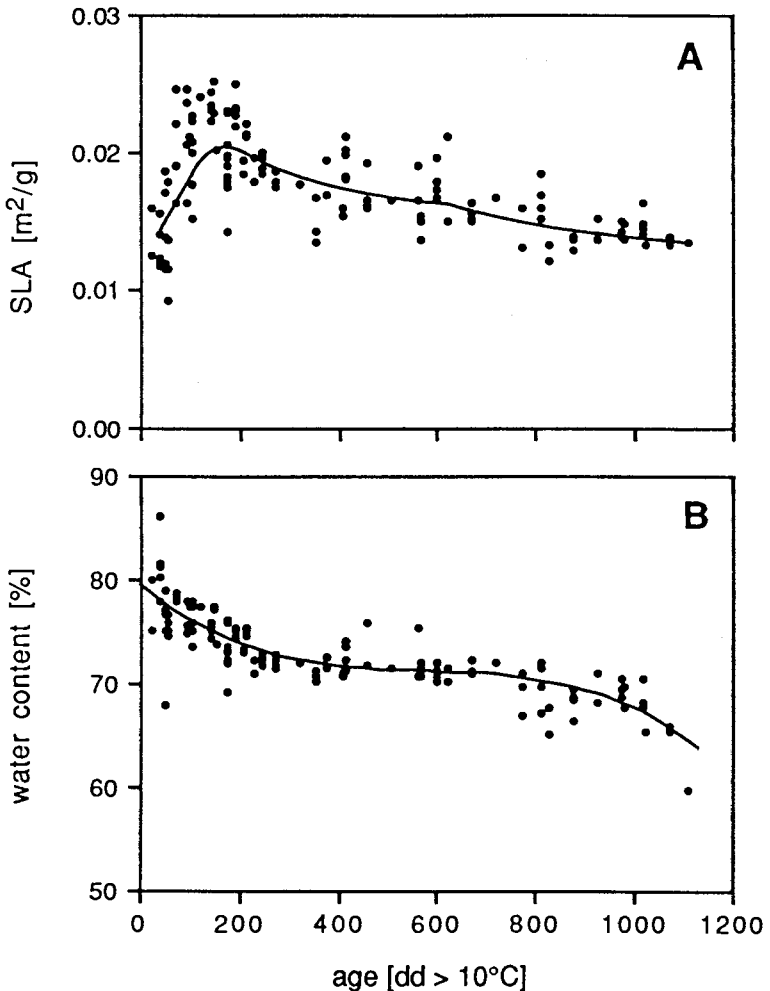


Fig. 2: Development of (A) specific leaf area index (SLA) and (B) water content of primary grapevine leaves depending on their individual age. — Regressions: (A): Lowess smoother (CLEVELAND 1985); (B): $y = 79.56 - 4.04E-2x + 6.73E-5x^2 - 3.89E-8x^3$, $r^2 = 0.71$.

Verlauf des (A) spezifischen Blattflächenindex (SLA) und (B) des Wassergehalts von Primärblättern bei Weinreben in Abhängigkeit von ihrem individuellen Alter.

6 %. However, this content decreased quickly in leaves reaching maturity. When the leaves were fully expanded (250 dd, Fig. 1 A) the N level stayed at 3 % for most of the productive life span and declined again at leaf senescence. As far as the absolute amount of N is concerned (Fig. 3 B), a fast import of N takes place until leaf maturity, followed by plateau and a distinct export of N at leaf senescence. The N development of the lateral leaves is included in Fig. 6 B.

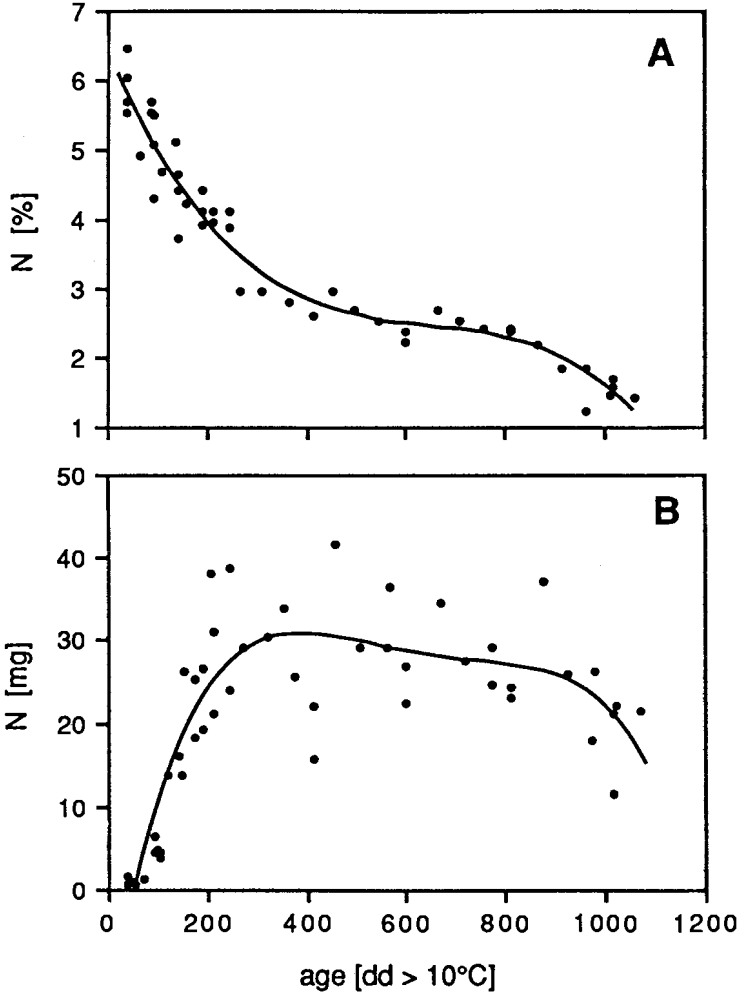


Fig. 3: Development of N concentration (A) and absolute N content (B) of individual primary grapevine leaves depending on their age. — Regressions: (A): $y = 6.45 - 1.69E-2x + 2.48E-5x^2 - 128E-8x^3$, $r^2 = 0.95$; (B): $y = -15.17 + 0.33x - 8.56E-4x^2 + 9.19E-7x^3 - 3.59E-10x^4$, $r^2 = 0.75$.

Verlauf der N-Konzentration (A) und des absoluten N-Gehalts (B) einzelner Primärblätter bei Weinreben in Abhängigkeit von ihrem Alter.

The consequence of these leaf growth rates is the realized overall dry matter production during one season, expressed in Fig. 4 on a per shoot basis and separated into primary and lateral leaves. The losses due to summer pruning are concealed by the growth during the period between the sampling dates. Comparing the number of primary and lateral leaves, Fig. 4 A evidences that lateral leaf number soon outstripped

primary leaves and was 3.5 times higher at the end of September. The lateral shoots were induced by the topping in late May, whereas the production of new primary

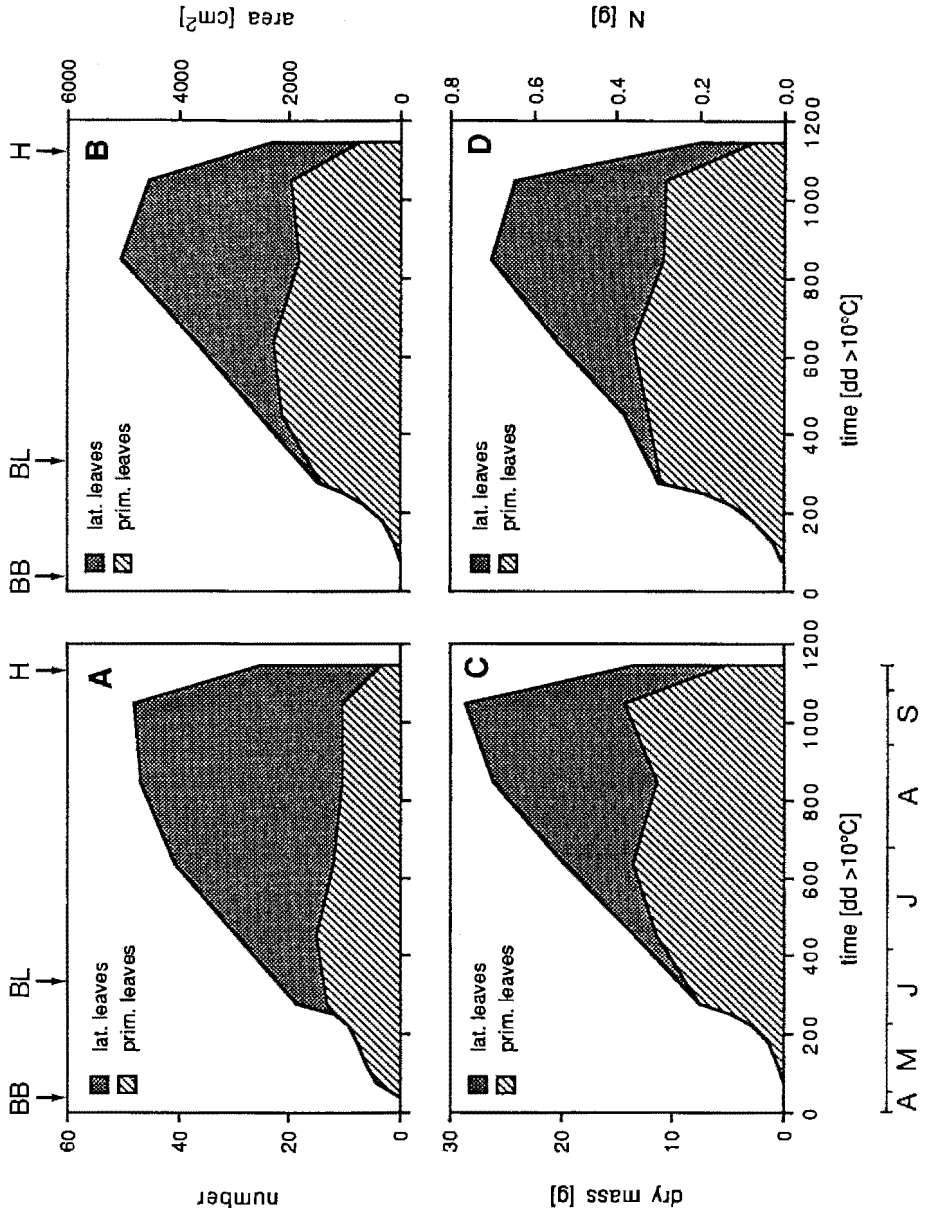


Fig. 4: Number (A), leaf area (B), dry mass (C), and absolute N content (D) of primary and lateral grapevine leaves per shoot during the season (arrows: BB = budbreak, BL = blooming, H = harvest).

Jahreszeitlicher Verlauf von Anzahl (A), Blattfläche (B), Trockengewicht (C) und absolutem N-Gehalt (D) von Primär- und Geizblättern je Trieb bei Weinreben (Pfeile: BB = Austrieb, BL = Blüte, H = Ernte).

leaves was stopped. The comparison of leaf area (Fig. 4 B) and leaf mass (Fig. 4 C) per shoot with leaf number (Fig. 4 A) indicates that lateral leaves did not grow to the same size as primary leaves. Total lateral leaf area was only slightly higher than primary leaf area, and lateral leaf mass equalled primary leaves in September. For N content, the same distribution (Fig. 4 D) between primary and lateral leaves is observed as for dry mass. Total leaf mass produced per shoot peaked at 29 g. While primary leaf number declined after 400 dd (Fig. 4 A), primary leaf mass still increased (Fig. 4 C), due to the continuing slight growth of the primary leaves (cf. Fig. 1 B).

Shoot and grape growth

Shoot growth rates were proportional to leaf growth rates. Fig. 5 shows the strong correlation between total shoot dry weight and total leaf dry weight per vine. The

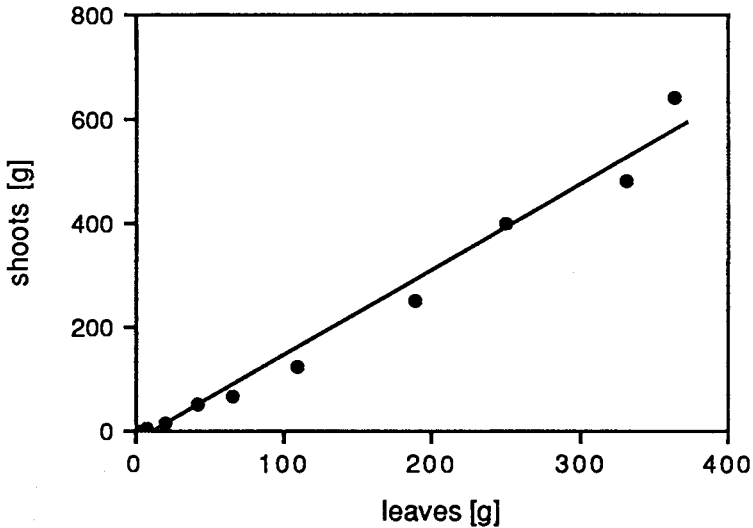


Fig. 5: Correlation between dry mass of shoots and leaves of grapevines before beginning of leaf fall. — Regression: $y = -20.29 + 1.64x$, $r^2 = 0.98$.

Korrelation zwischen Trockengewicht von Trieben und Blättern bei Weinreben vor dem Blattfall.

increase of shoot mass amounted to about 1.6 times the rate of leaf mass increase. Of course this is only valid prior to commencing leaf fall. The dry weight development of the reproductive units (weighed as clusters) was very slow as inflorescences before blooming (at 335 dd) and increased shortly after starting auxin production (ALLEWELDT 1977) to an average rate of $0.4 \text{ mg} \cdot \text{dd}^{-1}/\text{berry}$, reaching a final berry weight of 273 mg. This resulted in 63 g of grapes/shoot. Primary shoot water content (Fig. 6 A) fell markedly, after a short increase at the beginning, from 90 % to a low level of 55 % at harvest, due to lignification. The water content curve for the lateral shoots (graph not shown) coincided in shape and magnitude with the one for the primary shoots. The water content of the grapes approached a peak of 90 % at approx. 600 dd and subsequently declined to 80 % at harvest or, reversely expressed, the content of solids (sugars) increased.

The course of the N concentration of shoots and grapes is depicted in Fig. 6 B. Grape N content started at a high value comparable to young leaves (cf. Fig. 3 A) and ended at approx. 1 %. Lateral shoots followed the same pattern as primary shoots, but

the newly initiated lateral shoots started growing with a higher N content than exhibited by the primary shoots at this point in time. The weak increase of the N level in primary shoots at the end of the season is presumably due to the reallocation of N from senescent leaves to the N reserves in the lignifying shoots.

Total grapevine production

Since productivity is highly dependent on variety, climate and cultivation practices, relative rather than absolute dry matter and N distributions are presented (Fig. 7;

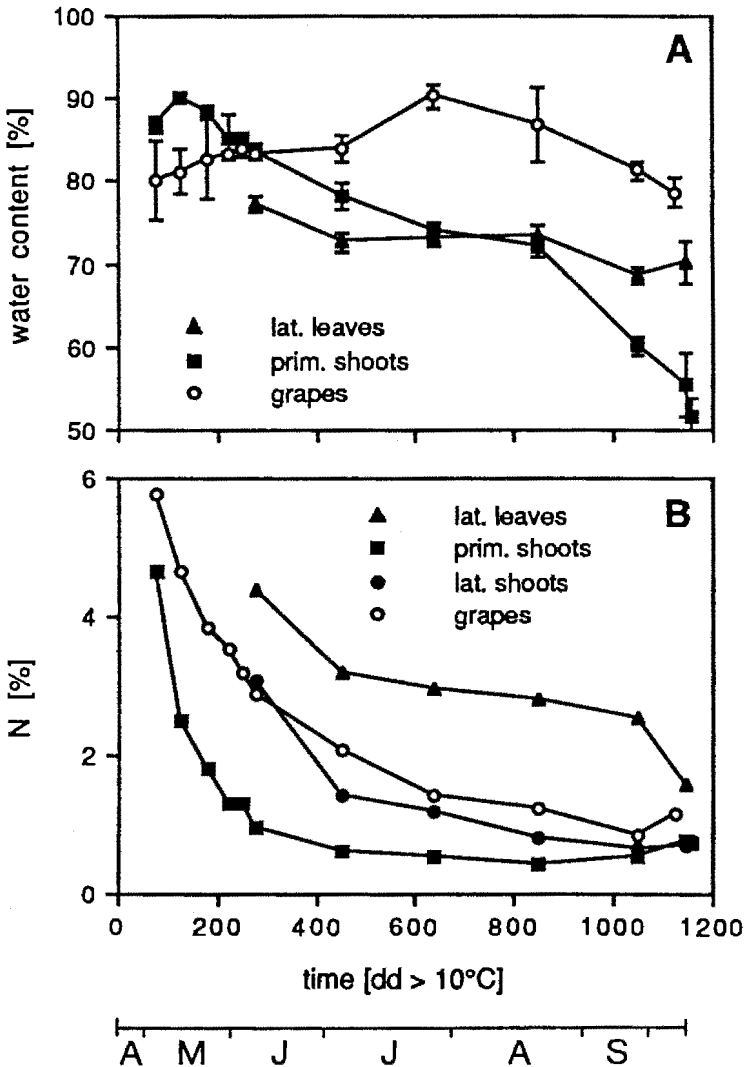


Fig. 6: Average water content (A) and N concentration (B) of grapevine leaves, shoots and grapes during the season. — Bars in (A) indicate standard deviation.

Jahreszeitlicher Verlauf des durchschnittlichen Wassergehaltes (A) und der N-Konzentrationen von Blättern, Trieben und Trauben (B) von Weinreben.

phenological and cultivation events are indicated by arrows). In this manner the changing proportions of the mass of different plant organs during the growing season become more obvious. A mean number of 14.2 shoots/vine and 1.8 grape clusters/shoot (field data) was used. There was a clear difference between dry matter (Fig. 7 A) and N (Fig. 7 B) allocation. Most of the photoassimilates were directed to the shoots, which were outweighed by grapes only at harvest time. Shoot mass and leaf mass were more or less balanced until 500 dd. In contrast, by far the greatest amount of N was located in

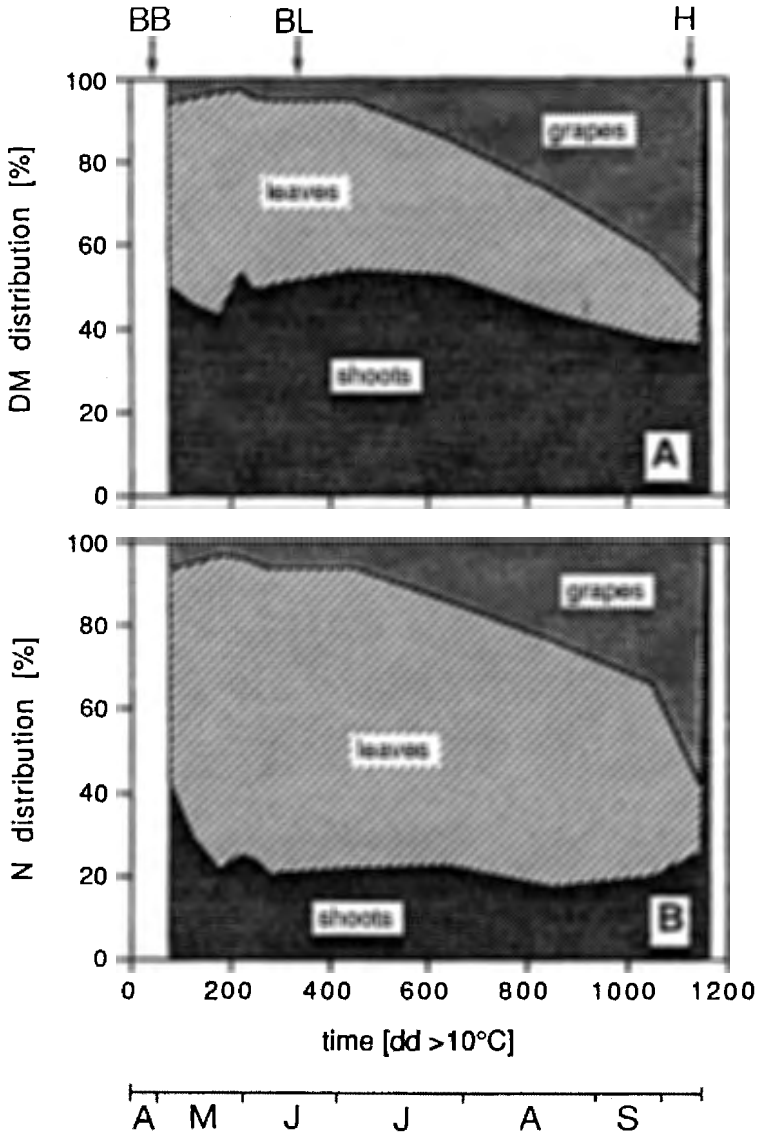


Fig. 7: Relative distribution of (A) dry matter (DM) and (B) nitrogen in the annual above ground organs of grapevines (arrows see Fig. 4).

Relative Verteilung von (A) Trockensubstanz (DM) und (B) Stickstoff in den oberirdischen, einjährigen Organen von Weinreben (Pfeile s. Fig. 4).

the leaves during much of the season, surpassed only by grapes at harvest. The proportion of N found in the shoots remained remarkably constant (approx. 20 %). The allocation of dry matter and N to grapes occurred to an equal extent. At harvest fruit dry matter yielded 50 % of the total newly grown above-ground mass. In terms of absolute numbers per vine, the maximum leaf number and mass at 1050 dd attained 607 and 364 g, respectively, maximum leaf area and leaf N at 845 dd were 6.40 m² and 8.9 g, respectively, and the grape yield at harvest was 797 g (82 °Oechsle = 19.8 °Brix).

Discussion

The use of degree-days instead of days as time scale has the advantage of normalizing temperature as a driving variable for growth. Phenological events of different years cannot be compared with each other basing on calendar time. The dd concept, however, allows a multi-seasonal comparison of growth rates, phenological temperature driven events (CHRISTENSEN 1969), as well as quality aspects (KOBLET and ZWICKY 1965), since it operates on the basis of accumulated heat above the developmental threshold of the plant. Ideally, if temperature were the only driving variable, i.e. at unlimiting conditions (radiation, nutrition, water etc.), the same phenological events in different years should coincide.

The first two leaves expanding simultaneously at budbreak reach only half the size and weight of the following primary leaves, which grow to an average leaf size of 200 cm² and 1.5 g. Leaf development is divided into two phases: a rapid growth phase of about 250 dd, followed by a plateau in leaf area as well as N and water content. Only leaf weight still slightly increases. Similar findings were reported by CARBONNEAU (1976) and HUGLIN (1986). KRIEDEMANN *et al.* (1970) observed maximum photosynthesis of leaves 30–35 d after unfolding at their full size, which corresponds to an age of 250 dd in July or August. After full expansion a period of approx. 650 dd follows, indicated by the N and water content, where the leaves are in a productive condition. The divergence of leaf area and weight of mature leaves is also reflected in the continual decline of the specific leaf area after 250 dd. Since in this phase the N concentration steadily decreases, it must be photoassimilates that cause the further, slow increase in weight until leaf abscission. SLA has the same temporal pattern for all primary leaves, irrespective of their formation time. During the first 150 dd SLA increases, i.e. at the beginning more is invested in producing photosynthesizing leaf area than in gaining weight. At the age of 900 dd, the leaves become senescent evidenced by a sudden decrease in water and N content. WILLIAMS (1987 a) found a linear decline of SLA during the season for Thompson Seedless grapevines. The lowest SLA of 0.014 m² · g⁻¹ obtained at the end of the season compares well with our results.

The N concentration of vegetative as well as reproductive tissues starts at a high level, sharply declining to a relatively constant level thereafter. This trend is commonly reported in literature (e.g. ALEXANDER 1957; BETTNER *et al.* 1986; WILLIAMS 1987 b). Since the observed tissue concentrations comprise both young growing zones and aging (lignifying) parts, the following explanation for the dynamics of N concentration is proposed: newly formed tissue zones (leaf and berry increments, shoot tip growth) are generated at a high N concentration (6–7 % N), but immediately after an export of N sets in. The measured average N content of the organ (leaf, shoot, grape) is determined by the balance of newly formed N rich tissue and old low N tissue. As the season advances, the older tissue predominates, thus lowering the average N content. The rate of N exported out of aging tissues is affected by the plant's stress situation (e.g. N deficiency). The N thus mobilized is reallocated to other tissue being generated or to reserves (cf. WERMELINGER *et al.* 1991).

The comparison of primary and lateral leaf data shows that lateral shoots contribute considerably to canopy area, as well as to mass. However, lateral leaves never reach the size of primary leaves, exceeding them in numbers but not in mass. At the end of the season, leaf area, dry matter and N content were distributed in equal proportions to primary and lateral leaves. Lateral leaves can contribute a substantial amount of carbohydrates for grape ripening (KOBLET 1969; KOBLET and PERRET 1971). The proportion of lateral and primary leaves is strongly affected by the summer pruning practices.

The relative distribution of dry matter in a grapevine differs from the distribution of N. More dry matter is allocated to shoots than to leaves, but more N is located in leaves than in shoots. About an equal proportion of dry matter and N is present in grapes.

Summary

In an established vineyard, samples of leaves, shoots, and grapes were taken at regular intervals throughout the season. Fresh and dry weight, leaf area, water and nitrogen content were determined and the growth rates expressed on a degree-day $> 10^{\circ}\text{C}$ (dd) basis. Primary leaf growth was divided into two phases. A rapid growth of $0.0043\text{ g} \cdot \text{dd}^{-1}$ up to the age of 250 dd was followed by a continual slight increase of $0.0006\text{ g} \cdot \text{dd}^{-1}$ until leaf abscission. At 250 dd the leaves were fully expanded and N import was completed. After a short increase, the specific leaf area ($\text{m}^2 \cdot \text{g}^{-1}$) steadily declined with age. N and water concentrations decreased in all aging organs. In late summer, the lateral leaves outnumbered the primary leaves; however, total area, dry matter and N content of leaves were equally distributed. The relative distribution of dry matter and N in leaves and shoots differed. The highest proportion of N was present in leaves, while most dry mass was accumulated in shoots.

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