

Carbon relations and competition between woody species in a Central European hedgerow

IV. Growth form and partitioning

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Summary. Growth of woody species has two components, one pertaining to increment of biomass, the other to the architectonic arrangement of dry matter in space. Only the combination of both components explained the competitive strength of species that dominate in different stages of a hedgerow succession in Central Europe. Biomass increment was measured using an empirical volumetric method, and plant architecture was investigated from branching patterns which determined the growth form of species. Assimilate partitioning was determined from total plant carbon gain and biomass increment in different above-ground plant parts. Those species with lower dry matter, nitrogen, and phosphorus costs for occupying and shading space during canopy development were the stronger competitors and replaced pioneers, even though their rate of CO₂ uptake was low. Ecological implications of different partitioning patterns for the survival of a plant and for successional changes in vegetation are discussed.

In the previous papers of this series it was shown that the competitive ability of species and their distribution and dominance within a hedgerow vegetation, representing several stages of a secondary forest succession, could not be explained by photosynthetic characteristics at the leaf level. Pioneers had the highest photosynthetic capacity and the highest annual carbon gain, but, despite this, they were replaced by mid-successional or climax species with lower photosynthetic capacity and carbon gain (Küppers 1984a, c). Therefore other factors in relation to carbon gain must be important during competitive replacement of species and successional changes in vegetation.

Ecological successions, defined as orderly, reasonably, directional, and therefore predictable, processes of community development resulting from modifications of the physical environment by the community itself (Odum 1969), often show general trends, such as increasing species diversity, biomass, productivity, and stock of nutrients in tissues (Odum 1971; Drury and Nisbert 1973; Horn 1974; Whittaker 1975a, b; Golley 1977). Succession has been described as a stochastic plant-by-plant replacement process (MacArthur 1958; Horn 1975), but this description does not help to understand the mechanisms involved. Plant interactions are evident, but information on these is limited (Newman 1983).

During succession different factors may become impor-

tant to plant existence, allowing different species and growth form types to dominate in certain stages. For example, formation of thorns as a protection against browsing may be important for pioneers, whereas specific canopy structures may be more efficient in later phases of succession (Horn 1971). In this paper assimilate partitioning, branching patterns, and crown formation are investigated in relation to utilization of carbohydrates. Representative species, dominating in different stages of a hedgerow succession as part of a forest succession in Central Europe, were chosen.

Materials and methods

A general description of the hedgerow site (in Northern Bavaria), the climate (temperate) and of the field gas exchange system used for continuous tracking of CO₂ and H₂O exchange under natural conditions of leaves attached to the twig was presented by Küppers (1984a). The hedgerow community, a Rhamno-Cornetum (Passarge (1957), 1962), was described in detail by Reif (1983).

1. The experimental species

The species investigated are representative of different stages of a natural, secondary succession (definition by Horn 1974; Whittaker 1975b) from fallow land to beech forest in Central Europe. Woody pioneers are *Rubus corylifolius* (blackberry) and *Prunus spinosa*. Early and mid-successional species are the hybrid *Crataegus × macrocarpa* (hawthorn) and *Acer campestre* (field maple). In the long term all species were replaced by the common beech, *Fagus sylvatica*, representing the climax community. *Ribes uva-crispa* (wild gooseberry) is a species of the understory of hedgerows. All species are winter-deciduous.

2. Determination of biomass of individual plants and an analysis of error

The dense canopy of a hedgerow and the high number of competitive woody plants causes strongly asymmetrical growth forms. Therefore the shape of an individual plant and its light environment have to be taken into account when calculating standing biomass and plant carbon budgets. In the following approach this is demonstrated for *Acer campestre*. The stem of a plant was divided into vertical 1-m sections starting from the ground. For plants growing in the side canopy of a hedgerow with a laterally devel-

oped crown, first order branches were subdivided into 0.5 m sections, each section representing a light zone (Fig. 1A), while for plants growing into the canopy crown only vertical light zones were defined (Fig. 1B; I: fully exposed, II:

half shaded, III: half shaded to shaded, IV: completely shaded). During expansion of the vegetation, zone IV is enlarged as soon as all other zones are complete.

The procedure for calculating total above-ground biomass of an individual plant from the length of the stem, the length of first- and second-order branches and the leaf biomass in different light zones is described in Fig. 2. The axis volume of single branches was determined from a statistically linear relationship ($r^2 = 0.95$) between the diameter of a shoot axis and the distance from the tip of the shoot; a twig could thus be treated as a cone and its volume calculated from its length. Another linear relationship ($r^2 = 0.98$) was used to determine dry matter of an axis from its volume.

The total number of third-order twigs was calculated from a linear relationship with the length of the second order main branch ($r^2 = 0.84$); combining this relation with the relative frequency of twig length (Fig. 3) yielded the total number of third-order twigs within a certain length class. Samples indicated that the linear relationship and the frequencies in Fig. 3 remained constant for higher branching orders. Thus it was possible to determine the total dry matter of all twigs of fourth and higher branching order belonging to a third-order branch system by using chained integration (example in Küppers 1982).

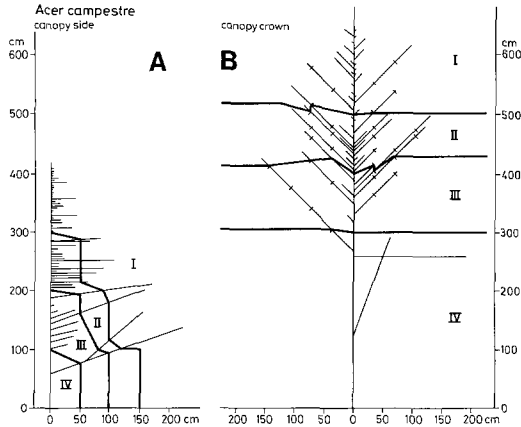


Fig. 1A, B. Diagrammatic representation of growth forms of *Acer* plants from the canopy side (left) and the canopy crown (right) used for the calculation of biomass and total plant carbon budget. Light zones I to IV represent the light regime under natural conditions of growth. For further explanations see text

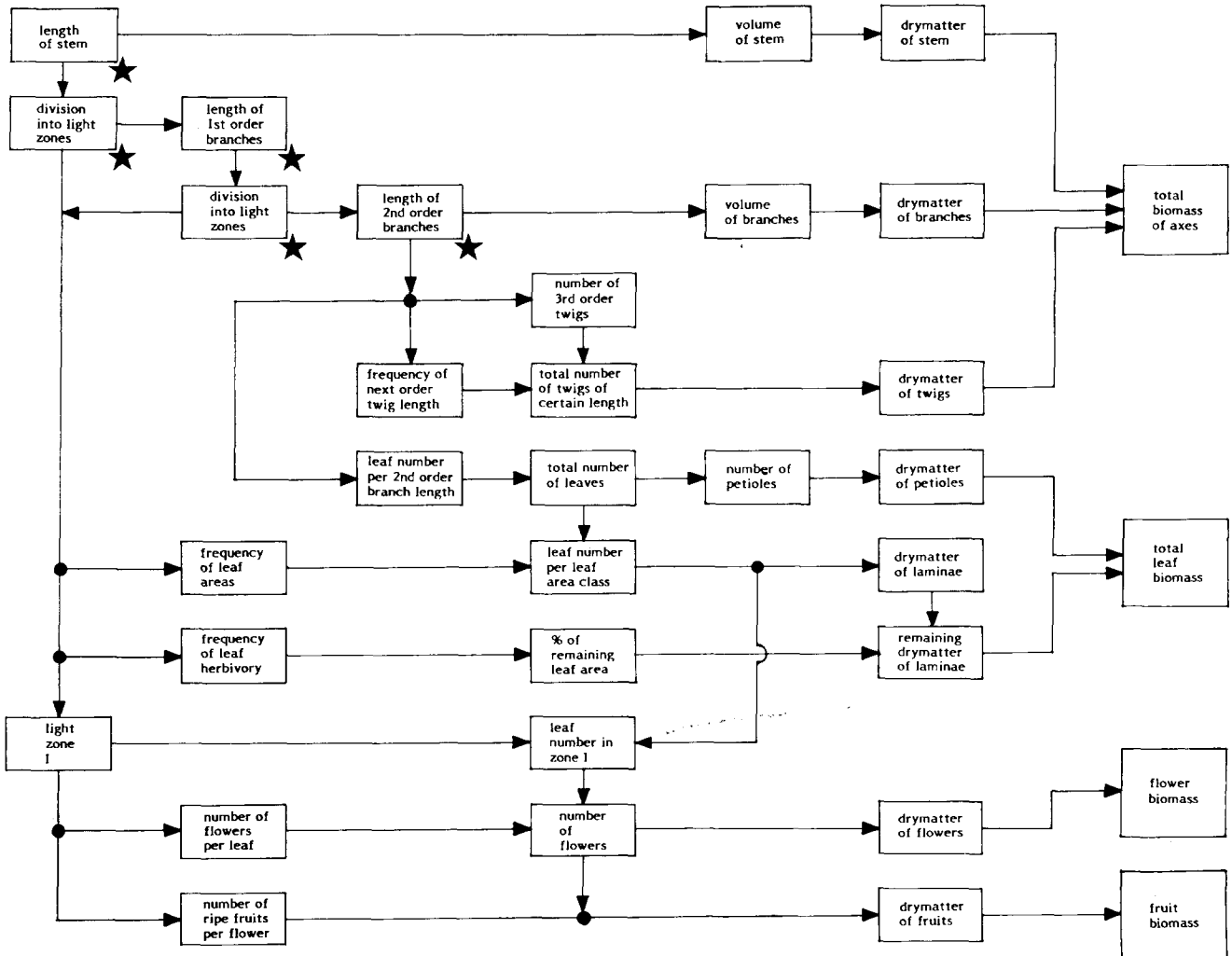


Fig. 2. Flow-chart for the calculation of standing crop. Starred parameters had to be determined independently in order to calculate increase in standing crop between two seasons. Further explanation is given in text

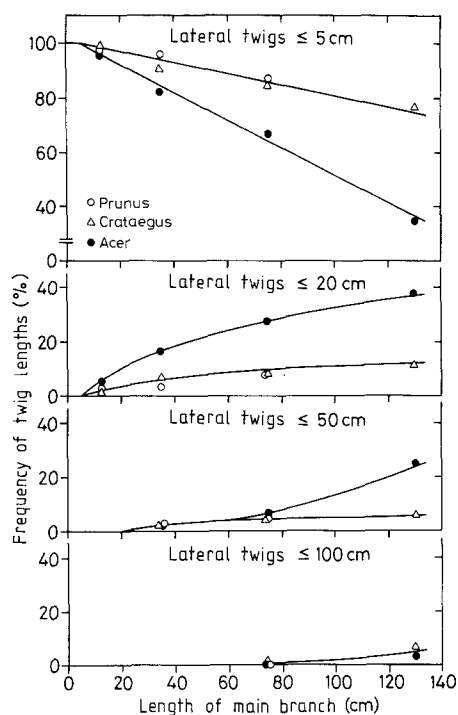


Fig. 3. Frequency of twigs of certain lengths as related to the length of the main branch (3rd or higher branching order) on which they insert. The sum of all frequencies at a given main branch length corresponds to 100%. Each symbol represents the mean of a main branch length class with $x \leq 5$ cm, $5 < x \leq 20$, $20 < x \leq 50$, $50 < x \leq 100$, or $100 < x \leq 160$ cm. For *Prunus* no branches of 3rd order were longer than 100 cm. Further explanation in text

The total number of leaves developed in a twig system with the main branch of second order was calculated from a polynomial regression with second-order branch length as independent variable ($r^2 = 0.81-0.89$). With decreasing light the number of leaves per branch length decreased. The distribution of leaf size (in leaf area classes) was obtained from samples of fully expanded leaves. Combining the dry matter/leaf-area relationship for the different light zones with leaf sizes yielded the potential dry matter of laminae. From this the percentage of herbivory had to be subtracted: this was obtained from a comparison of measured leaf area with the calculated potential area using a quadratic function relating length of midrib and projected area.

Fully developed flowers were found only in zone I, so it was possible to utilize a flowering factor (number of flowers per leaf) and a fruiting factor (number of ripe fruits per flower) in order to calculate flower and fruit biomass.

Detailed data and a test of the procedure are given in Küppers (1982). Absolute errors were in all cases less than 13% for biomass of branch axes (mean $4.9\% \pm 3.4$), less than 9% for leaf number ($5.0\% \pm 2.6$), 14% for laminal dry matter (mean $6.2\% \pm 4.3$), 15% for petiole dry matter ($7.1\% \pm 4.6$) and 10% for total biomass ($3.7\% \pm 2.7$).

3. Determination of seasonal dry matter increase

The annual length increment of a shoot was linearly correlated with the original twig length at the beginning of the season ($r^2 = 0.85-0.92$). From this the seasonal increase in biomass components could be calculated by the procedure

shown in Fig. 2. If fruiting and flowering was similar in two seasons, only the five starred parameters had to be changed in the flow chart.

As a test, single plants were measured at the end of the first season and the biomass was predicted for the second. At the end of the second season plants were harvested and compared to the predicted values. Errors in all cases were similar to those given above.

4. Determination of plant carbon gain and assimilate partitioning

The total seasonal carbon gain of an individual plant was calculated from the annual carbon budget of sun leaves (Küppers 1984c), from the mean total leaf biomass during the season, and its distribution within the light zones. Problems of describing the light regime (Anderson 1964, 1966) and the effect of leaf inclination (Kriedemann et al. 1964) were simplified by assuming the same annual carbon balance for every leaf within a certain light zone. Though the diurnal gas exchange patterns were different depending on leaf inclination, representative measurements indicated similar daily carbon balances for different leaves, and therefore similar annual carbon balances. Thus carbon budgets (per unit of lamina dry matter) in zone I amounted to 100%, those in zone II to 93% of sun leaves, zone III to 30%, and those in zone IV were negligible. This is similar to what was found in *Fagus sylvatica* (Schulze 1970). Using a transformation factor of 0.66 (after Larcher 1980) carbon gain was converted to dry matter gain.

The seasonal increase of stem and twig biomass of individual plants, and the seasonal leaf production, were correlated with the dry matter gain from photosynthesis (Table 1A); from this the partitioning of assimilates was calculated by assuming that the partitioning into roots was the remainder of carbohydrates not used in increase of above-ground biomass.

5. Determination of species-specific leaf area index, crown volume gain and light transmission through the canopy

About 15 km of hedgerows were assessed by eye for the maximum species-specific leaf area index. In parts of hedgerow communities where a single species dominated and formed a relatively homogeneous horizontal canopy, the leaf area index (LAI) was determined by calculating the projected leaf area from the measured length of every leaf found within a vertical column in the canopy of 1 m^2 ground area (error of leaf area determination was 5%). Canopy edge effects on LAI were avoided. Measurements were taken in August, when leaf expansion was finished and leaf fall was minimal.

Crown volume gain was determined from crown surface areas (sun crown) of about 20 m^2 for a mature, mono-specific stand of high LAI. As crown expansion is not homogeneous from year to year, a period of three growth seasons was investigated. Radial crown expansion was determined as vector length from surface to stem or crown centre. The surface was defined by tips of the outer twigs. Thus, volume gain could be calculated from annual radial expansion per previous season's crown surface. Knowing the dry matter of newly grown axes in this volume, volume gain per dry matter could be calculated. From the total annual CO_2 input of an individual and the number of newly

grown twigs in the outer canopy (light zone I), volume gain per carbon balance (in $l\text{ g}_{\text{CO}_2}^{-1}$) could be determined.

Crown volume gain per nutrient (N, P) investment was determined by relating volume gain per dry matter to the nutrient contents of this dry matter (leaves and branches). It is assumed that nutrient content per unit dry weight in young twigs is similar to that in leaves, since young twigs have a high portion of green tissue. This agrees with data for *Loranthus europaeus* (Schulze et al. 1984), which had 20 mg nitrogen $\text{g}_{\text{DW}}^{-1}$ in leaves and current year twigs, a value similar to that obtained for leaves in the species investigated here (Küppers 1984a). It also agrees with data for ash contents in leaves and cortex tissues presented by Larcher (1980).

Annual water vapour loss per occupied volume was determined for a sun-exposed branch of 70 cm length assuming that, in the outer canopy, leaves did not significantly affect each other's water vapour transfer into the surrounding air space. Annual transpiration per unit leaf area was taken from Küppers (1984c).

Light transmission through the canopy was determined in August 1982 for a clear and an overcast day in the stands used for determination of LAI. Measurements were done within 1 h before and 1 h after solar zenith using several quantum sensors (Licor Nebraska, 400–800 nm) arranged within 1 m² below the densest part of the canopy. Calculated transmission values (in per cent of day light) include the time and ground area integrated means. Repeated measurements on different days and localities resulted in similar values and errors.

Results

1. Distribution of species within the hedgerow vegetation

A crown projection map of the hedgerow investigated (Fig. 4), a Rhamno-Cornetum (see Reif 1983), shows a patchwork of woody individuals. At an early stage of secondary succession (Fig. 4A, central and lower part of graph), where pioneers, such as *Rubus* (Rub) and *Prunus spinosa* (Ps) have invaded fallow land, the canopy is incomplete and open, and there is only one crown layer. Light, at this stage, is not an interspecific competitive factor, since growth is not limited by shading from the crowns of neighbouring plants, but by climatic conditions (Küppers 1984c).

Invasion of fallow land neighbouring hedgerows occurs quickly (one to a few years, depending on the distance from the hedge) by vegetative migration of the pioneers. However, at this stage there is selective pressure from browsing by animals, and successful pioneers (*Rubus*, *Prunus*, *Rosa*) are protected either by thorns or by spines. They create the appropriate conditions for the establishment of successional species, as they weaken the competitive ability of grasses by shading, and protect seedlings from herbivory. An early successional species is *Crataegus* (Cr in Fig. 4), mid-successional species are *Acer* (Aca) and *Prunus avium* (Pa).

In later stages of succession the canopy closes, and several crowns overlap but usually do not infiltrate each other. Figure 4B shows a stage where early- and mid-successional species (*Crataegus*, *Acer*) dominate in the canopy. Crowns of individual plants are often enlarged towards the canopy sides, and the stem base often falls outside the crown projection area of an individual. This indicates high competitive

pressure for light. Pioneers are already shaded out from the centre, and only the remains of dead individuals indicate their former existence. A typical understory species, *Ribes* (Ri in Fig. 4) was shown to be restricted to this site by its water relations (Küppers 1984b).

General trends of succession are indicated: species diversity and standing biomass (the latter is indicated by crown sizes) are larger in the later successional stage (Fig. 4B). If successional development could proceed without disturbance, the hedgerow vegetation would be replaced by a beech (*Fagus sylvatica*) forest, starting from the older part of the vegetation (canopy crown) towards the younger hedgerow sides. Hedgerows are usually cut in cycles of 20–40 years, so a natural climax community cannot develop.

Successional changes in hedgerow vegetation are paralleled by changes in growth form of species. This will be investigated in the following sections in which I will discuss how branching patterns determine growth form, and how growth form in relation to carbon gain may affect competition for light in mature plants.

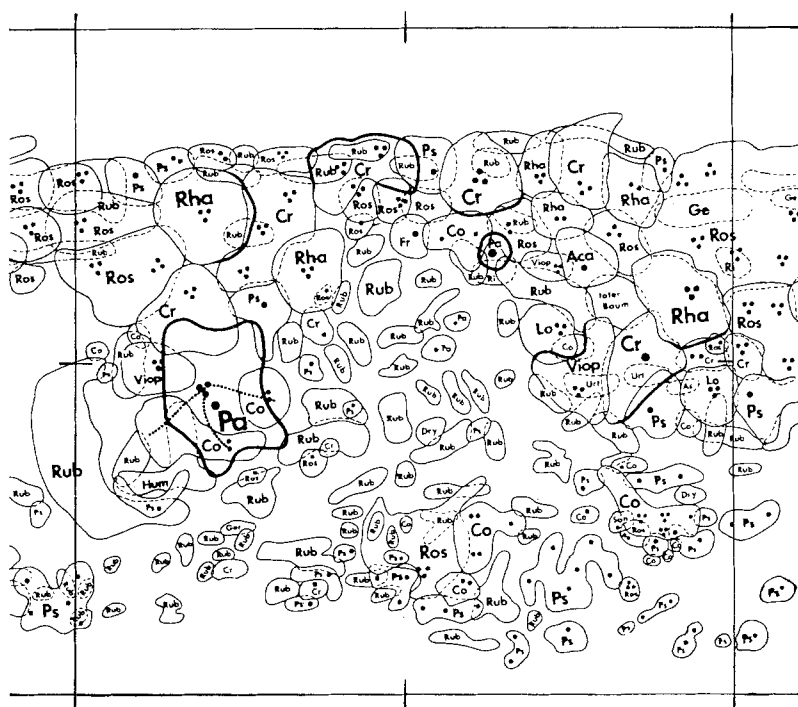
2. The significance of branching pattern for the growth form

Several aspects appear to be important in competition for light, such as rate of growth, crown architecture, distribution of leaf surfaces within the crown, and the height to which a plant can grow. To understand crown architecture, it is essential to investigate the branching patterns of species.

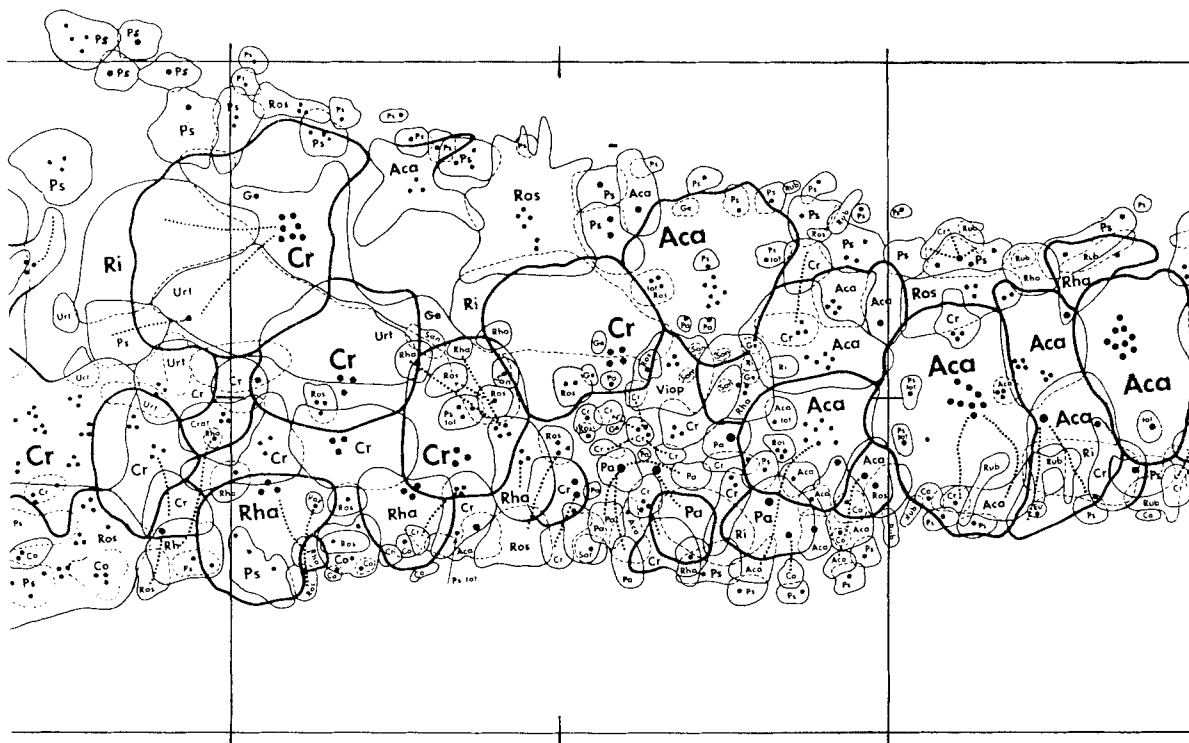
The growth of European trees and shrubs can be characterized by the longitudinal (along the vertical axis) and by the lateral (along the horizontal axis) symmetry (Fig. 5). In longitudinal symmetry lateral twigs are promoted either at the top (acrotony), the middle portion (mesotony) or at the base (basitony) of the main branch axis, while in lateral symmetry growth of twigs is promoted either at the upper (epitony) or lower (hypotony) side of the main branch (Troll 1937; Rauh 1950).

The species-specific combination of these symmetries determines plant growth form (Fig. 6). Shrubs are characterized by basitony combined with epitonic branching of lateral shoots. The main axis stops growing, and buds at the stem base develop lateral branches of greatest length while apical branches remain short (*Rubus*, *Rosa*, *Ribes*). This contrasts with tree-like species and trees which develop a stem in all cases (*Prunus spinosa*, referred to as *Prunus* in the following, *Crataegus*, *Cornus*, *Acer*) as a result of promoting growth of apical branches (mesotony or acrotony). However, in "tree-shrubs" (*Prunus*, *Cornus*) lateral symmetry is epitonic and lateral twigs usually overgrow the main branch. As lateral axes of higher orders branch in the same way the canopy does not gain in height but develops more laterally. "Shrub-trees" (*Crataegus*) branch both epitonically and hypotonically, and therefore they have an intermediate position between "tree-shrubs" and trees. In trees (*Acer*) already existing branches are not overtopped by newly grown twigs, because of the hypotonic development of high-order branches. The stem retains its function as leading axis, continuously gaining in height while lateral main branches continuously gain in distance from the stem, enlarging the crown projection area.

These branching patterns result in different growth responses under competitive pressure for light (Fig. 7). In isolated *Prunus* a short, stunted shrub-tree results. Shading



A



B

Fig. 4A. Map of projected crown areas of woody and herbaceous species of a portion of a hedgerow. *Thick solid lines*: dominant canopy; *thin solid lines*: subcanopy; *broken lines*: understorey. *Dots* indicate single twigs.

A younger successional stage on fallow land.

B older successional stage with a closed canopy.

Aca: *Acer campestre*, *Co*: *Cornus sanguinea*, *Cr*: *Crataegus × macrocarpa*, *Dry*: *Dryopteris filix-mas*, *Eu*: *Euonymus europaeus*, *Fr*: *Frangula alnus*, *Ge*: *Geranium robertianum*, *Hum*: *Humulus lupulus*, *Lo*: *Lonicera xylosteum*, *Pa*: *Prunus avium*, *Ps*: *Prunus spinosa*, *Rha*: *Rhamnus cathartica*, *Ri*: *Ribes wacrispa*, *Ros*: *Rosa canina*, *R. subcanina*, *R. vosagiaca*, *Rub*: *Rubus corylifolius* agg., *San*: *Sambucus nigra*, *Urt*: *Urtica dioica*, *Viop*: *Viburnum opulus*, *tot*: dead, *toter Baum*: dead tree. Squares correspond to 20 × 20 m². Further explanation in text

may increase length of single branches and may promote growth of upright renovation twigs, but does not change the branching pattern. Thus *Prunus* is limited in height gain (observed maximum: 4–5 m). It evades shade by producing suckers.

Crataegus (Fig. 7) shows a similar development, but hypotony as well as epitony is found (Fig. 5), so that a tree-shrub results. Under shade, epitonic shoots may reach api-

cal dominance and considerable length (3–4 m, Fig. 7), taking over stem characteristics and carrying the individual crown into the canopy of an expanding vegetation (maximum observed height: 6–8 m).

Acer (Fig. 7) has a steadily growing trunk and height gain is independent of situation, whether isolated or in competition for light. The species advances into the canopy crown of the vegetation through the crowns of pioneers. It repre-

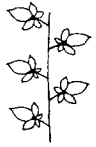
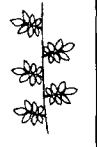
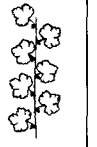
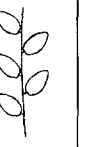
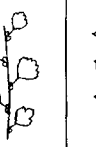
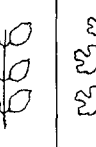
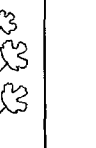



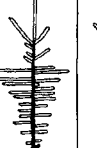

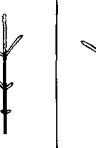
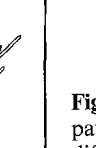


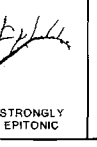
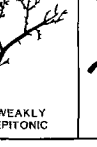


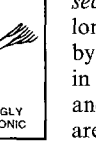
	<i>Rubus</i>	<i>Rosa</i>	<i>Ribes</i>	<i>Prunus</i>	<i>Crataegus</i>	<i>Cornus</i>	<i>Acer</i>
Phyllotaxy							
	ALTERNATE	ALTERNATE	ALTERNATE	ALTERNATE	ALTERNATE	OPPOSITE	OPPOSITE
Branching pattern	SYMPODIAL	SYMPODIAL	SYMPODIAL	SYMPODIAL	SYMPODIAL	MONOPODIAL	MONOPODIAL
Longitudinal symmetry							
	BASITONIC	BASITONIC	WEAKLY BASITONIC	MESOTONIC-ACROTONIC	MESOTONIC-ACROTONIC	MESOTONIC-ACROTONIC	MESOTONIC-ACROTONIC
Lateral symmetry							
	STRONGLY EPITONIC	STRONGLY EPITONIC	STRONGLY EPITONIC	WEAKLY EPITONIC	EPITONIC & HYPOTONIC	WEAKLY EPITONIC	STRONGLY HYPOTONIC

Fig. 5. Phyllotaxy, branching patterns, and branching symmetry of different woody hedgerow species. *Filled sections* for longitudinal symmetry: 1-year-old branches, *open sections*: current year branches. The longitudinal symmetry is determined by the branching pattern of a shoot in its second year (after Troll 1937 and Küppers 1982). Opposite leaves are oriented decussately

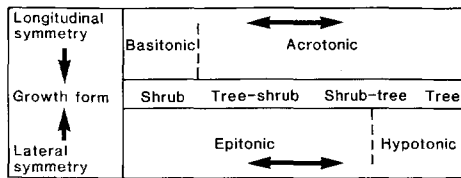


Fig. 6. Principles of bud development, growth form symmetry and resultant growth form in woody plants (after Troll 1937 and Küppers 1982). Further explanation in text

sents typical tree characteristics (observed maximum height: 12 m) as also found in the beech (*Fagus silvatica*, not shown: height up to 40 m).

The pioneer *Rubus* (Fig. 5) is a liane, by the definition of Ellenberg and Mueller-Dombois (1967). Its runners are short-lived and grow horizontally if not supported. They flower in the second year and die back after maturity. The species cannot replace other woody species for lack of a crown, but it efficiently evades shade by taking root outside a closed canopy (up to 6 m per year).

3. Assimilate partitioning within the plant

Küppers (1984a, c) showed that pioneer species had a higher carbon gain per unit of leaf than mid-successional or climax species. This indicates differences in the efficiency of using assimilates for growth. The plants investigated were of different ages (Table 1A), but were in all cases mature and non-senescent. Therefore it was possible to compare assimilate partitioning for plants of different life span and growth form. The partitioning pattern was determined from the data in Table 1A.

In all species about 10% of carbohydrates were invested in formation of leaves (Table 1B) independent of whether they grew as trees (*Acer*, *Crataegus*), as shrubs (*Prunus*, *Ribes*), or as a liane (*Rubus*). Shrubs invested 10% more dry matter in formation of twigs than trees, whereas trees used 10% more dry matter in stem growth. At high fruit

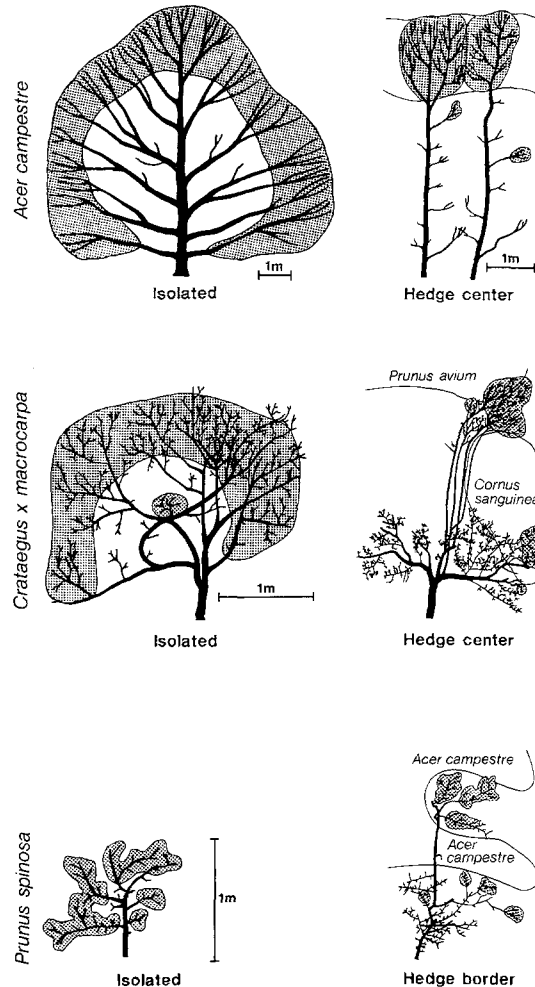


Fig. 7. Growth of *Acer campestre* (top), *Crataegus x macrocarpa* (middle row) and *Prunus spinosa* (bottom) without competition as isolated plants and under competitive pressure of neighbouring plants. *Shaded area*: region of leaves of the investigated species

Table 1A. Plant age, total leaf biomass, annual dry matter gain from photosynthesis, above-ground biomass increase per plant and primary production rate (total annual dry matter gain per unit leaf dry matter) in two successive seasons. Individual plants were mature and dominant in the successional stage they represented

	Plant age in 1981 (years)	Total leaf dry matter produced in 1981	Total projected leaf area in August 1981	Total flower and fruit biomass produced in 1981	Annual dry matter gain in 1981	Total above- ground biomass increase in 1981 (including leaves and fruit)	Twig and stem biomass in autumn 1980	Primary production rate
	(a)	(g)	(m ²)	(g)	(g)	(g)	(g)	(g g ⁻¹ a ⁻¹)
<i>Rubus</i>	1	13.2	0.17	—	112	32	—	8.5
<i>Prunus</i>	7	64.7	0.68	63.5	675	466	376	10.4
<i>Crataegus</i> ^a	12 (13)	435.3 (713.1)	5.02 (8.22)	262.1 (2,529)	4,442 (6,727)	3,154 (4,871)	2,157 (3,072)	10.2 (9.4)
<i>Acer</i>	13	690.6	9.00	—	4,912	3,390	5,867	7.1
<i>Ribes</i>	9	30.7	0.50	15.8	371	261	188	12.1

^a In () at high fruit yield

Table 1B. Partitioning of assimilates within the plant (%) for the same individuals as in Table 1A

	Leaves	Twigs	Stem	Roots ^a	Flowers and fruit
<i>Rubus</i>	12	—	17	71	—
<i>Prunus</i>	10	45	5	31	9
<i>Crataegus</i> ^b	10 (11)	35 (22)	20 (3)	29 (26)	6 (38)
<i>Acer</i>	14	34	21	31	—
<i>Ribes</i>	8	46	12	30	4

^a Including root and stem respiration

^b In () at high fruit yield

yield (*Crataegus*, Table 1B), fewer assimilates were partitioned into stem and twig biomass. In all species except *Rubus* about 30% of carbohydrates flowed to below-ground plant parts.

The results indicate that trees support height gain, shrubs lateral expansion (and formation of thorns grown as short twigs; not shown), and the liane storage of assimilates in roots (Rauh 1938) which gives a high regeneration capacity for growth of short-lived runners. These patterns may vary depending on fruit yield.

4. The significance of branching pattern for the occupation of space

Height gain allows a species to survive in an expanding canopy, but it does not necessarily enable dominance by shading-out of competitors. Dominance depends on crown formation, a process in which carbohydrates are utilized for the occupation of space. In the following the efficiency of crown formation will be investigated.

In addition to the branching patterns, crown characteristics depend on the reach of twig systems. Figure 3 shows the relative proportion of lateral twigs of certain length classes in relation to the length of a main branch from which they grow. In all species the relative amount of short twigs decreases with increasing branch length, whereas the frequency of longer twigs increases. For *Prunus* and *Crataegus* the fractions change very similarly, whereas in *Acer* the relative proportion of short twigs is generally lower

and the proportion of longer twigs generally higher for any given branch length. Obviously *Acer* grows twig systems with a greater reach than *Crataegus* or *Prunus*. Additionally twigs of *Acer* grow in length faster than those of *Crataegus* and *Prunus* (Table 2A).

One cannot deduce directly from this how much dry matter is used in crown formation, therefore the space occupied and structured per unit of dry matter was investigated in two ways. Firstly, the volume occupied by representative branch systems was determined by combining species-specific branching patterns (Fig. 5) with number of twigs (calculated from a linear relationship between branch length and number of lateral twigs; Küppers 1982) and frequency of certain twig length classes (Fig. 3). As a representative length of the branch systems 70 cm were chosen (Fig. 8), since for this length branch age was more than 1 year (2–3 years) in all species, so that lateral twigs were already formed. It was assumed that leaves occupied a cylinder since they inserted either alternately or decussately (Figs. 5 and 8). From this the volume occupied by each twig could be calculated. The twigs falling into the space of another twig were not counted for volume increase but for increase in dry matter. The result is shown in Table 2A. Single twig systems of *Prunus* gain the smallest volume per unit invested dry matter and those of *Acer* the largest. The same sequence is found when volume gain is related to invested nitrogen or phosphorus (Table 2A).

Secondly, this result was tested using crown increment. A volume gain of 0.200 m³ per m² crown surface per year was obtained for *Acer* (*Crataegus*: 0.175 m³m⁻²a⁻¹, *Prunus*: 0.149 m³m⁻²a⁻¹). Knowing the number of new twigs in this volume (*Acer*: 321, *Crataegus*: 704, *Prunus*: 1,056) and their mean dry weight, the newly-grown twig dry matter per newly-occupied crown volume could be determined. The result confirms the information obtained on the single twig system level: *Acer* gains the most crown volume per invested dry matter, nitrogen, or phosphorus, and *Prunus* the least (Table 2B).

Besides the occupation and structuring of space by twigs the density of leaves is important for light competition. Table 2A shows the projected leaf area per volume for the twig systems in Fig. 8, calculated from statistical relationships between twig system length and number of leaves (Küppers 1982). The highest density was found in *Acer*, a medium

Table 2A. Rate of shoot elongation, efficiency of branch volume gain with respect to biomass, N and P, and leaf density and water loss per branch volume of competing woody species. Seasonal rate of shoot elongation was measured for the 50 longest current-year shoots at the end of the season in a crown surface of 20 m². For further explanation see text

	Single branch					
	Rate of shoot elongation (cm a ⁻¹)	Volume gain per dry matter investment (leaves + branches) (ml g ⁻¹)	Volume gain per nitrogen investment (leaves + branches) (ml mg _N ⁻¹)	Volume gain per phosphate investment (leaves + branches) (ml mg _P ⁻¹)	Density of leaf area (cm ² l ⁻¹)	Annual water vapour loss per occupied volume (mol a ⁻¹ l ⁻¹)
<i>Prunus</i>	30 ± 14	38	1.8	21.1	235	139
<i>Crataegus</i>	47 ± 13	78	3.8	32.5	258	338
<i>Acer</i>	57 ± 11	134	6.9	70.5	364	22
<i>Fagus</i>	—	549 ^a	—	—	—	—

^a According to Schulze et al. (in press)

Table 2B. Efficiency of crown volume gain with respect to biomass, N, P and total plant carbon balance, and leaf area index, together with transmission of light in the dense canopy of competing woody species. Further explanations in the text

	Crown level							
	Newly grown twig dry matter per newly occupied crown volume (g m ⁻³)	Volume gain per dry matter investment (leaves + branches) (m ³ kg ⁻¹)	Volume gain per nitrogen investment (leaves + branches) (m ³ g _N ⁻¹)	Volume gain per phosphorous investment (leaves + branches) (m ³ g _P ⁻¹)	Volume gain per photosynthetic carbon gain of entire plant (l g _{CO₂} ⁻¹)	Leaf area index (m ² m ⁻²)	Transmission of light (%)	
							bright day	overcast day
<i>Prunus</i>	269	3.7	0.17	2.1	1.09	3.8	6	7
<i>Crataegus</i>	125	8.0	0.39	3.3	1.12	8.5	2	3
<i>Acer</i>	97	10.3	0.53	5.4	2.31	8.9	2	2
<i>Fagus</i>	—	—	—	—	—	6.0 ^a	—	—

^a according to Ellenberg (1978)

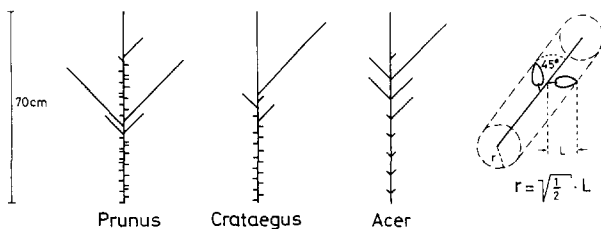


Fig. 8. Modelled branching pattern of representative branch systems in *Prunus*, *Crataegus*, and *Acer*. In order to define the volume occupied by the branch system an imaginary cylinder was positioned around the axis of every single twig, its radius being given by the leaf length. Further explanation in text

density in *Crataegus*, and the lowest in *Prunus*. A similar result was obtained for the measured maximum LAI (Table 2B) and consequently for light transmission measured on a bright and on an overcast day (Table 2B).

Knowing the carbon input of an individual (Table 1A) and its crown volume gain, it was possible to determine the space occupied by the crown for each unit of assimilated carbon dioxide (Table 2B). Again this was highest in *Acer* and lowest in *Prunus*. But despite a higher leaf density in *Acer*, its water vapour loss per occupied volume of a representative branch in the outer canopy was much smaller than that of the other species (Table 2A).

Discussion

Carbon gain is essential for growth, and the amount of carbon gained determines increment in biomass. This functional relationship is commonly used in modelling growth (e.g. Schulze 1982; Jarvis and Leverenz 1983; Penning de Vries 1983). Other functional relationships are indicated by the data in Table 1B. For example, the proportion of carbohydrates partitioned into leaves was similar in all species independent of growth form and independent of the actual carbon input of the individual plant investigated. This indicates that a certain percentage of photosynthesizing tissue is necessary to support respiring plant parts. Another relationship is indicated by the fraction partitioned into roots which was about 30% in all species except *Rubus*. To support above ground plant parts with water and nutrients, and to keep transpiration and nutrient demand for growth balanced (Richards and Rowe 1977a, b) a certain root/shoot biomass ratio is essential (Brouwer 1963, 1983; Wareing 1970) which may not change in trees even over several years (Chalmers and Van den Ende 1975). Therefore, these patterns of partitioning should be caused by physiological, functional needs of balancing uptake rates with rates of demand.

The stem/crown partitioning ratios are obviously more independent of the physiological partitioning patterns. They appear to have adaptive importance in a particular

environment. For example, the development of a crown near the ground, as found in pioneers, may involve the formation of thorns as protection from browsing and therefore leaves less carbohydrate for stem growth. On the other hand crown formation at a greater height depends on stem production, but then thorns are no longer essential in the crown after reaching a certain distance from the ground. Hence more assimilates are available for stem growth. However, transitions exist between these extremes (e.g. *Crataegus* as a thorn-protected shrub-tree and *Cornus* as a thornless tree-shrub).

A special case is *Rubus* growing by runners and partitioning 70% of carbohydrates into below-ground plant parts. It is unlikely that this partitioning pattern is for physiological reasons. Indeed Rauh (1938) observed large amounts of starch grains packed in below-ground parts which indicates that they function as a storage organ. This again appears to be of significance: those carbohydrates are safe from browsing as well as fires (frequently-burnt hedgerows usually contain a higher proportion of *Rubus*), and they are available for regrowth of runners. Regrowth is essential in this pioneer, as near the ground it will very likely be overgrown by other species.

It was shown (Table 2) that, with respect to leaf area density, light interception, volume gain per unit of dry matter, nitrogen, phosphate, or CO₂, and with respect to water loss per occupied volume, mature plants of *Acer* were more efficient than *Crataegus*, and the latter more efficient than *Prunus*. Therefore the mid-successional *Acer* appeared to be the stronger competitor (after seedling establishment and the early phase of growth where crowns are open) compared to the early successional species, *Crataegus* and *Prunus*. Consideration of the volume gain per dry matter in the climax species *Fagus sylvatica* (on twig system level, Table 2A) shows an even more efficient use of assimilates than in *Acer*. Similar results are indicated in *Fagus* for the volume gain per carbon assimilated and for the water loss per unit of volume, though exact amounts are not known. They follow from the especially low carbon balance and water loss on the leaf level (Küppers 1984c) and the especially high volume gain per dry matter (Table 2A). *Fagus* therefore outgrows and shades out the other species during succession.

The efficiency of crown formation may be related to nutrient use in successional stages. Bazzaz (1979) and Bazzaz and Pickett (1980) pointed out that pioneers in forest succession have higher photosynthetic capacities than mid-successional or climax species, which was also found for the species investigated in this series (Küppers 1984a, c). Species with a lower photosynthetic capacity should need less nitrogen, since photosynthetic capacity is closely linked to nitrogen contents of leaves (Chapin 1980; Mooney 1980; Field et al. 1983). In secondary succession, nutrient availability may decline during vegetation development (Daubenmire 1968), thus later successional species could have a competitive advantage since they have lower nitrogen demands for carbon gain and crown formation. A lower water vapour loss per occupied volume may also be an advantage in a condensing vegetation, since during succession towards a forest the water table may be lowered and water availability may decline.

Species distribution in Fig. 4 appears to be the result of the combination of physiological and morphological characteristics separating pioneer "niches" and "niches"

of later successional species. Pioneers have means of quick invasion of open land [in the species investigated vegetative organs such as runners (*Rubus*) or suckers (*Prunus*)] but low ability to compete for light. They may be termed as "spatial competition avoiders", but as a result of physiological responses at the leaf level (low shade tolerance, Küppers 1984a) they are non-invasive in existing woody plant communities. Therefore these species are mainly found alongside a hedgerow canopy or on open fallow land (Fig. 4). The migration efficiency then determines early and later pioneers: *Rubus* can grow 6-m long runners in one season, while *Prunus* migrates only 50 cm per season (Willmanns 1975). Successional species are indicated by shade tolerance, a pre-requisite to establishment in a pioneer community, (*Acer*: Küppers 1984a; *Fagus*: Schulze 1972), and a high ability to compete for light. They are invasive in existing plant communities and are, therefore, found in older parts of a community (Fig. 4B).

A special case is the successional understory species *Ribes* which was investigated earlier in this series (Küppers 1984a, b). It can migrate by runners and is protected by spines, thus shows pioneer characteristics. For lack of a stable water budget under exposed conditions and for lack of sufficient shade tolerance it is limited to a half-shaded microsite within the hedgerow canopy. Limited light during the period of a closed hedgerow canopy is effectively compensated for by an extended growing season (Küppers 1984c). Thus the niche of this species depends on the vegetation but is that of a "temporal competition avoider".

Successional changes are often paralleled by changes in growth form spectra (e.g. Schmidt 1975) as a result of the replacing of species of a certain growth form by species of another growth form, rather than by changing growth habit of a species. This indicates that the frame of growth forms of one species, which may be called "life form", is likely to be genetically fixed and that the efficiency of growth forms is different in different stages of succession, due to differences in environmental conditions.

Acknowledgements. The investigations were supported by the Landesamt für Umweltschutz, Munich, in a project on "Ökologische Funktionsanalyse von Hecken und Flurgehölzen" (Schulze et al. 1982) and by the Sonderforschungsbereich 137 of the Deutsche Forschungsgemeinschaft. This is the last paper of a series resulting from the publication of a Dr. thesis. I wish to thank Prof. Dr. E.-D. Schulze (Bayreuth) for many helpful discussions and comments, and for the excellent facilities he placed at my disposal. I also wish to thank Prof. Dr. Meusel (Halle/Saale) for encouraging discussions on growth forms. I am grateful to Dr. I.R. Noble (Canberra) for critical comments and for correcting my English, and to Ms. I. Pleier, Mr. E. Wagenseil and Mr. J. Zeitler for their persistent help during biomass assessment.

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