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Light capture and Plant architecture determine Co-existence and Competitive Exclusion in Grassland Succession - and Grazing interferes in this process

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Abstract. Plants evolved in dense stands and thus competition for light has always been a strong selective pressure. Here we show that the pattern of biomass partitioning of a plant strongly affects its light capture efficiency. We also show how inherent plant architectural designs may constrain the plant's success of light capture when growing in dense vegetation. We show that these plant traits provide the mechanisms that allow some species to co-exist in the same stand of vegetation, while other species are competitively excluded from that vegetation. These mechanisms explain species replacement in a successional series. Finally, we show how grazing by deer interferes with the successional processes to the benefit of some species and the disadvantage of other species, depending on the constraints of their architecture and of their shade-tolerance features.

1 Introduction

The zonal vegetation of the temperate zone is broad-leaved, deciduous forest. Man's action has converted this forest into grassland and agricultural fields, over very substantial parts of its natural distribution area (ELLENBERG 1978, WHITFORD 1983). Under appropriate grazing loads or a suitable mowing regime these grasslands are largely stable in species composition over long periods of time. But if man's use of those derived plant covers stops, the vegetation gradually but readily turns into forest again. In this regenerative process shifts in species abundances occur, and some species are competitively excluded from the vegetation while other species maintain themselves as canopy dominants or as subordinate species in the understorey. What are the driving forces in this successional process? How do some plant species manage to increase in abundance and dominate while others fail? And how are some species excluded from the vegetation while others persist in a subordinate role? Finally, why is it that under grazing the successional processes appear not to work, or how does grazing interfere in the mechanisms of succession?

The single most important process in plant growth is photosynthesis. In fact, it is a complicated series of processes involving light harvesting, energy transport and carboxylation. In photosynthesis, plants harvest light to gain carbon and use these acquired assimilates to grow taller, reproduce, and respire. Accordingly, light harvesting always has been important to plants and, simply spoken, a plant with a larger total leaf area might be expected to harvest more light. But this simple rule does not necessarily hold, because plants have not evolved as totally free-standing individuals which simply had to increase their leaf area to capture more light. Throughout their long history plants generally have evolved in dense stands in which neighbours intensely compete for the available light. Thus, the efficiency of light harvesting always has been a strong selection pressure in plant evolution and differences in the efficiencies of light harvesting between species may determine their competitive success. As a consequence, it may also explain successional processes in vegetation.

Differences in light harvesting efficiencies between plant species have at least two macroscopical components: (1) Differences resulting from growth patterns of individual plants in a stand; species inherently differ in these growth patterns, and in competition with neighbours in a dense stand, some patterns may be more successful than others. But species also differ in their plasticity in growth patterns in response to the environmental conditions developing in a stand. (2) Inherent differences in the architectural designs of plants may constrain or favour the plant's light capture ability when growing in competition. In this paper we will show that these components, together with differences in the plant's physiological constraints that affect its shade-tolerance, provide the mechanisms that regulate species composition in stands of vegetation, and thus explain changes in a successional series from grassland to forest.

2 Light in vegetation canopies

In stands of vegetation leaves and other plant parts intercept the incoming light, and as a result the available amount of light attenuates from the top to the bottom of the vegetation canopy. More than half a century ago MONSI & SAEKI (1953) showed that the light distribution pattern in herbaceous plant canopies is strongly correlated to the pattern of leaf area distribution in the canopy and can be well described by a simple mathematical formula:

$$I = I_0 \cdot \exp(-kF_w) \quad \text{or} \quad ln\ I/I_0 = -kF_w \qquad (1)$$

Here F is the accumulative leaf area index (the amount of leaf area per unit ground area, LAI) from the top of the canopy until depth w. I_0 and I are the amounts of light (usually the photosynthetically active photon flux density, PPFD) on a horizontal plain above the canopy and within the canopy at depth w, respectively. k is the coefficient of light extinction in the canopy. k is calculated as the slope of the linear regression of I/I_0 after logarithmic transformation on F (see also HIROSE & TERASHIMA 2004). This relationship holds both for single-species and multi-species canopies (MONSI & SAEKI 1953, HIROSE & WERGER 1987, HIROSE et al. 1988, WERGER & HIROSE 1991, HIROSE & WERGER 1995).

Thus, the available light in the canopy decreases exponentially with the amount of leaf area passed (Fig. 2). Accordingly, tall plants which reach high in the vegetation canopy, can capture more light, but they have to invest more in biomass (stems, long and sturdy leaves) than short plants to attain a position high in the canopy. Short plants down in the canopy, on the other hand, can save on those biomass expenditures but they also capture relatively little light.

When we measure the distribution of leaf area of each species in the vegetation canopy we can calculate the amount of light harvested per species in the vegetation stand using the model of Hirose & Werger (1995): The light absorbed by the leaves of species i in the jth layer in the canopy (φ_{ij}) is calculated from

$$\varphi_{ij} = \mathrm{k} \cdot \mathrm{I}_0 \cdot \exp(-\mathrm{kF}_j) \cdot \Delta f_{ij} \qquad (2)$$

where Δf_{ij} is the leaf area of species i in layer j and F_j is the cumulative leaf area at layer j. Thus φ_{ij} can be determined from k and the distribution of leaf area of each species in the canopy. Total light absorbed by species i (Φ_i) then is given by

$$\Phi_i = \textstyle\sum_i \varphi_{ij} \qquad (3)$$

3 Plant biomass investment patterns and light harvesting efficiency

Since light is absorbed by leaf area, we may expect a positive correlation between light absorption and leaf area. This need not be a linear relationship, however, since leaves can overlap. Therefore, we may use a power equation to describe the relationship between light absorption and leaf area for each species in a stand:

$$\Phi = \mathrm{a\,A}^{\mathrm{b}} \qquad (4)$$

with Φ the total amount of light absorbed by the plant species, A its total leaf area, and a and b positive constants.

In order to acquire much light in a stand, a plant not just needs a large leaf area, but also has to position its leaves high in the canopy. Such plants must invest a large fraction of their biomass in support tissues such as stems. If we assume that plants largely develop their aboveground structure to absorb light, we may expect a positive correlation between Φ and the aboveground biomass as well, and may use another power function to describe the relationship between light absorption and biomass for each species in a stand:

$$\Phi = \mathrm{c\,M}^{\mathrm{d}} \qquad (5)$$

with M the aboveground biomass of the plant species and c and d positive constants.
Dividing equation (4) by A and equation (5) by M gives

$$\Phi_{\mathrm{area}} = \Phi/\mathrm{A} = \mathrm{a\,A}^{\mathrm{b-1}} \qquad (6)$$

and

$$\Phi_{\mathrm{mass}} = \Phi/\mathrm{M} = \mathrm{c\,M}^{\mathrm{d-1}} \qquad (7)$$

with Φ_{area} the light absorbed per unit leaf area defined for each species and Φ_{mass} the light absorbed per unit aboveground mass defined for each species. If M is considered the investment cost to absorb light, Φ is the benefit gained for that investment. Φ_{area} and Φ_{mass}, being the ratios of benefit to cost, can be considered efficiencies of using leaf area and aboveground biomass to absorb light (see HIROSE & WERGER (1995) where also further details of the calculation procedure for light capture are given).

We will use this model to analyse the characteristics of co-existence of species in a Dutch grassland, and to analyse the processes of vegetation succession, including shift in abundance and species replacement in a successional grassland series in Japan, with and without grazing.

In dense stands competition for light always is important. In competing for light in such dense stands, differences in plant stature may play a decisive role (WILSON 1988, ANTEN & WERGER 1996). Experimental and modelling studies have shown that plants that overtop their neighbours and display sufficient leaf area in the better-lit parts of the stand's canopy are usually the dominants in a stand (FLIERVOET 1984, HIROSE & WERGER 1995, PRONK 2004, PRONK et al. 2006, cf. MITCHLEY & WILLEMS 1995). To achieve this, biomass allocation patterns and associated light harvesting capacities are important (KÜPPERS 1985, HIROSE & WERGER 1995, ANTEN & HIROSE 1999). If constraints in plant stature do not allow a plant to reach the better-lit parts of the canopy, it may still be able to survive and grow under light-limiting conditions low in the canopy, provided that it is shade-tolerant. Here physiological mechanisms and plant morphologies allowing for increased light harvesting capacities play a role (KÜPPERS 1984, 1985, ANTEN & HIROSE 1999). We will demonstrate how these plant traits determine co-existence or species replacement in the Dutch and Japanese grasslands we analysed.

4 Species co-existence in a Dutch grassland

We analysed the species composition of a swampy grassland, the *Thelypterido-Phragmitetum* WESTHOFF & DEN HELD 1969 in the province of Utrecht, The Netherlands (HIROSE & WERGER 1995)(Fig. 1). For decades these swampy meadows have been mown annually in August to prevent succession towards swamp forest. Our stand contained 11 species (see Fig. 3, 4) ranging in height from 130 to 7 cm. *Phragmites australis* reached the highest levels in the vegetation canopy, with *Calamagrostis canescens*, *Carex acutiformis* and *Juncus acutiflorus* at middle height levels, and *Equisetum palustre*, *Scutellaria galericulata*, *Peucedanum palustre*, *Hydrocotyle vulgaris*, seedlings of *Salix cinerea*, *Veronica scutellata* and *Thelypteris palustris* in the lower layers.

Fig. 1: Stand structure of the *Thelypterido-Phragmitetum* in The Netherlands at peak above-ground biomass.

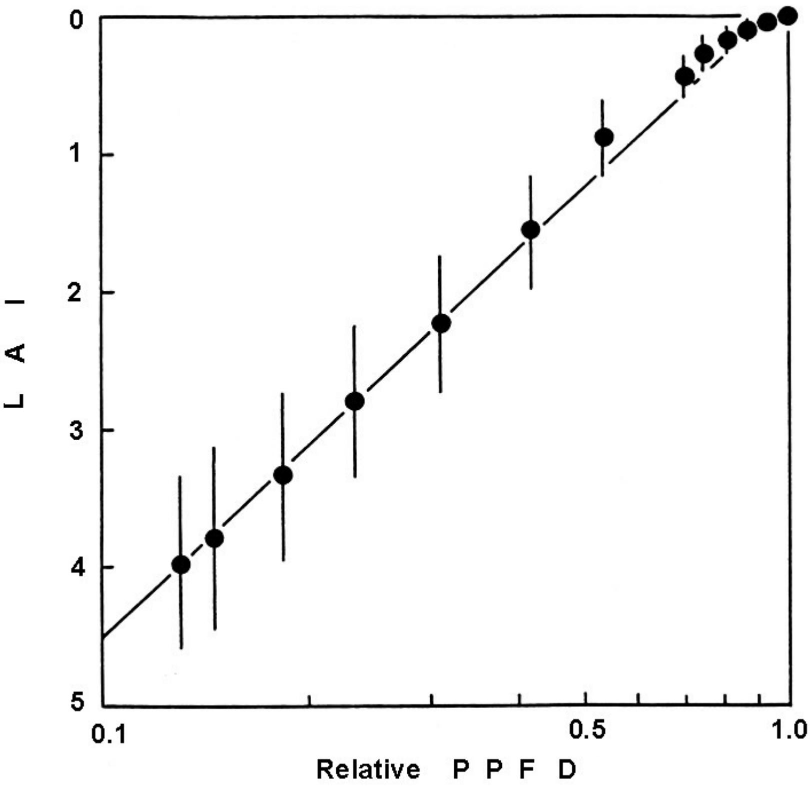
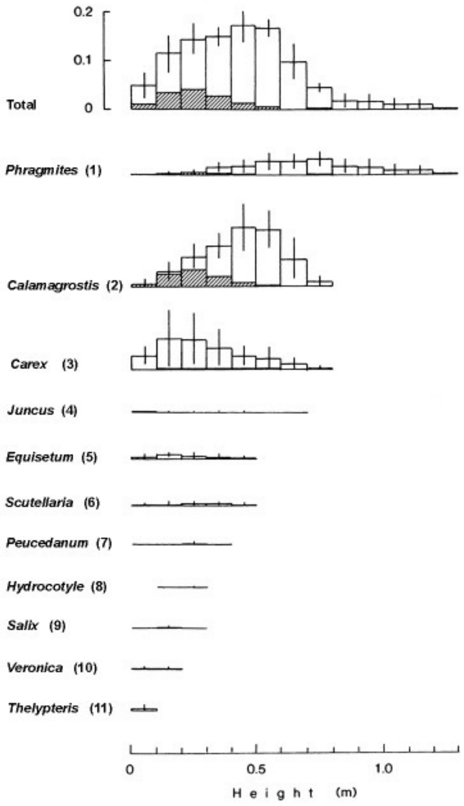


Fig. 2: Relationship between light (relative PPFD) in the vegetation canopy and the leaf area index (LAI) cumulated from the top of the canopy. Points where the amount of light in the canopy has been measured are shown together with 1 SD for the leaf area index at that point. x-axis is standardized: light just above the vegetation canopy = 1.00 (=100%).

We measured the light penetration through the vegetation canopy using light meters above and inside the vegetation. Subsequently we clipped the aboveground vegetation in layers of 10 cm height at peak standing crop, and using equations (1) through (3), we calculated light/leaf area relationship in the vegetation canopy (Fig. 2), the vertical leaf area distribution of all and each species in the vegetation canopy, and the vertical distribution pattern of the amount of light intercepted by each of the species (Fig. 3, 4). We found that the extinction coefficient k was 0.48 in this vegetation, which is clearly within the normal range for such grasslands (MONSI & SAEKI 1953, FLIERVOET 1984, ANTEN 1997). The total aboveground biomass was 407 $g \cdot m^{-2}$ with the three taller species *Phragmites*, *Calamagrostis* and *Carex*, comprising 35, 43 and 17 %, respectively, and all other 8 species together just 5 % of the total standing mass. Total leaf area index was 3.4 $m^2 \cdot m^{-2}$ with most leaf area concentrated in the middle layers of the vegetation canopy. *Phragmites* had most leaves in the upper, *Calamagrostis* in the middle, and

Carex in the lower layers of the vegetation canopy. *Phragmites* had 19, *Calamagrostis* 45, and *Carex* 30 % of all leaf area, and the other 8 species together just 6 %. Of all light falling into the canopy, 77 % was captured by the green parts of the canopy, 8 % by attached dead leaves, and 15 % reached ground level, where mosses grew. Of the total incoming light the green parts of *Phragmites* absorbed 23, *Calamagrostis* 37, and *Carex* 14 %, and the other 8 subordinate species together 3 % (Fig. 4).



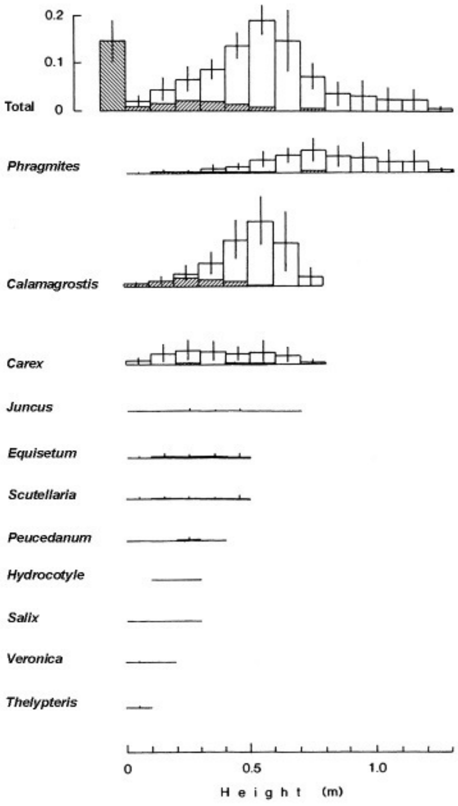


Fig. 3 (l): Vertical leaf area distribution of 11 species in the *Thelypterido-Phragmitetum* and of the total vegetation. Shaded areas are values for dead leaves. Horizontal axis represents height (m) above ground level. Vertical axis represents leaf area in relative values (total leaf area =1)

Fig. 4 (r): Light intercepted by 11 species in the *Thelypterido-Phragmitetum* and by the total vegetation. Shaded areas are values for dead leaves. Horizontal axis represents height (m) above ground level. Vertical axis represents absorbed light (PPFD) in relative values (total absorption = 1).

Using the data and equations (4) through (7), we calculated the investments (costs), benefits and efficiencies of light capturing for all species (Fig. 5, 6). Light absorption increased more than proportionally with increasing leaf area of the species (b > 1) and proportionally with increasing biomass (d was not different from 1.0). Thus, for these species, increasing their total leaf area gave more benefit in terms of amount of light captured than increasing their aboveground biomass. Among the species Φ_{area} increased significantly with increasing leaf area, but Φ_{mass} was not significantly correlated with total aboveground mass (Fig. 6). Thus, the efficiency of light capture measured per unit leaf area increased as species grew more leaf area, and these were in our stand the taller, dominant species with much of their leaf area reaching relatively high in the vegetation canopy. However, the efficiency per unit biomass did not increase as species grew more aboveground biomass, as Φ_{mass} was not necessarily large for those tall species.

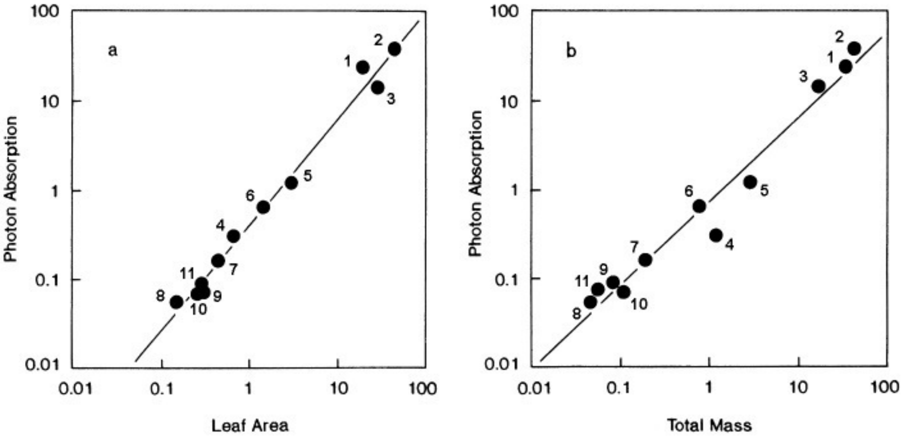


Fig. 5: Relationships between captured light (photon absorption) and leaf area (a) or aboveground biomass (b) of 11 species in the *Thelypterido-Phragmitetum* (indicated by dots; species numbers as in Fig. 3). Axes are in relative values: total captured light = 100; total leaf area = 100; total aboveground biomass = 100.

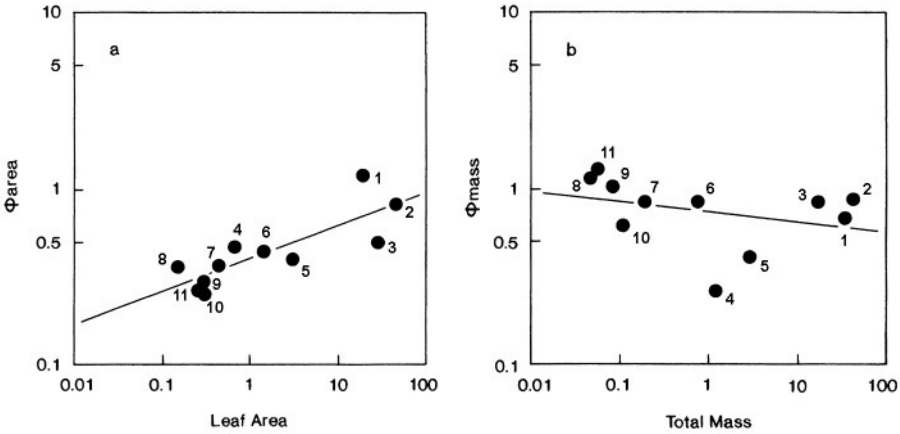


Fig. 6: Relationships between light absorbed per leaf area, Φ_{area}, and leaf area (a) and between light absorbed per aboveground mass, Φ_{mass}, and aboveground mass (b) of 11 species in the *Thelypterido-Phragmitetum* (indicated by dots; species numbers as in Fig. 3). Axes are in relative values.

Accordingly, the three taller species could dominate the canopy because they captured most of the incoming light, and they could do so, because they grew much of their leaves relatively high in the canopy. This gave them high light capture efficiencies per unit leaf area, but in order to achieve this they had to invest a large proportion of their biomass (in supporting tissues such as stems or sturdy, long leaves), and this reduced their light harvesting efficiency per unit biomass. The subordinate species, while capturing relatively little light in absolute terms and therefore having a rather low efficiency of light capture per unit leaf area, nevertheless captured their light with equal or sometimes higher efficiency per unit biomass as the taller species. They could do so, because they invested relatively large proportions of their aboveground biomass into the production of leaves and they tended to make thin leaves: the specific leaf areas (SLA, area of green leaf per unit of leaf mass) of the subordinate *Hydrocotyle* and *Thelypteris* were up to 4 fold larger than those of *Phragmites* and *Carex*. Although specific leaf area values in nearly all species vary phenotypically according to the growth conditions of the species, to a large extent the ranges in these values are species-specific (genotypically determined) (LAMBERS & POORTER 1992).

Our results show that the taller species dominating the vegetation stand have different biomass allocation strategies for light capture than the subordinate species in the lower parts of the vegetation canopy. This allows all these species to persist in the different light environments that are characteristic along the height of the vegetation canopy. While the subordinate species capture relatively little light and cannot reach the high layers of the canopy, they can persist in the shady lower part of the vegetation canopy because of their high Φ_{mass} and probably their low light compensation points. This explains their shade tolerance. The taller species, on the other hand, can maintain their dominance because of their high light capture, but they cannot also occupy the lower canopy layers by developing large leaf areas there, because of their low Φ_{mass} values and their higher light compensation points. This explains why species with so strongly different growth strategies can co-exist in the same stand.

5 Species replacement in a successional series of Japanese grasslands

Kinkazan is a small island close to the east coast of northern Honshu, Japan. Its climax vegetation is a broad-leaved deciduous forest of *Fagus crenata* and *Carpinus tschonoskii* and a mixed evergreen needle-leaved forest of *Abies firma* accompanied by *Carpinus tschonoskii, Zelkova serrata* and *Viburnum dilatatum* (MIYAWAKI 1987).

For centuries the island of Kinkazan falls within the precincts of the Koganeyama Shrine. In some large patches the forest has been destroyed and near the Shrine, forest regeneration has been prevented by the numerous grazing sika deer (*Cervus nippon*) which are protected on the island and have no predators locally. The sika deer have transformed those patches in closely cropped grazing lawns, dominated by the short grass *Zoysia japonica,* and they maintain them as grazing lawns for decades on end. Some large sections of these grazing lawns of up to 1 ha in size were fenced off for different lengths of time to exclude grazing. These exclosures, varying in age from 2.5 to 4.5 years, developed into a series of vegetation types of increasing plant height and aboveground biomass, and showed a gradual shift in species composition (Fig. 7, 8, 9). It was clear that ultimately the vegetation would regenerate to forest. We analysed the species composition of the different exclosures and light capture characteristics of the species using the methods presented above. We also investigated the architecture of the two most important species, the short, rhizomatous grass *Zoysia japonica* and the tall grass *Miscanthus sinensis*. With these data we demonstrate the mechanisms of species co-existence and species replacement and thus explain the successional process that is taking place (WERGER et al. 2002).

Fig. 7: *Zoysia*-grazing lawn at Kinkazan, Japan.

Our series contained the following four early successional stages:

- The *Zoysia japonica* grazing lawn that was permanently and heavily grazed by the sika deer (Fig. 7). They kept the vegetation homogeneously low but with a dense ground cover, strongly dominated by *Zoysia japonica*, but about 20 other species occurred, all with small to tiny plants, including some seedlings of *Miscanthus sinensis*. The vegetation was up to about 4 cm tall, with a few emergent leaves and flowering stems up to 8 cm tall. Total standing crop was about 150 $g{\cdot}m^{-2}$, and leaf area index 1.55 $m^2{\cdot}m^{-2}$.
- The *Hydrocotyle*-stands: a dense grassland that had developed from the *Zoysia* grazing lawn in 2.5 years. It was still strongly dominated by a dense *Zoysia* turf, also contained much *Hydrocotyle maritima* (some 10 % of the total aboveground biomass), and some 20 other species in smaller quantities, including a few small individuals of *Miscanthus*. The vegetation was about 30-40 cm tall. Total standing crop was about 445 $g{\cdot}m^{-2}$ and leaf area index was 3.91 $m^2{\cdot}m^{-2}$.

Fig. 8: *Miscanthus*-grassland after several years of protection from grazing.

- The *Brachypodium*-stands: up to 65 cm tall grassland that had developed out of a *Zoysia* grazing lawn under 4.5 years of exclusion, on a somewhat dry, gentle slope. This vegetation was less dense than the *Zoysia*- and *Hydrocotyle*-stands. *Miscanthus sinensis* and *Brachypodium sylvaticum* were dominants, *Zoysia* was scarce. Total species number was about 20. Total standing crop was about 240 $g \cdot m^{-2}$ and leaf area index was 1.82 $m^2 \cdot m^{-2}$.
- The *Miscanthus*-stands: about 180 cm tall, dense grassland that developed out of the *Zoysia* grazing lawn, also under 4.5 years of protection from grazing, but at a damp, gentle footslope. *Miscanthus sinensis* dominated. Tall herbs, grasses, sedges, shrublets, climbers and a number of small, subordinate species were present, but *Zoysia japonica* had disappeared. Total species number was about 27. Total standing crop was about 945 $g \cdot m^{-2}$ and leaf area index was 6.05 $m^2 \cdot m^{-2}$ (Fig. 8).

Though the *Brachypodium-* and *Miscanthus*-stands do not differ in length of deer exclusion, but differ in edaphic conditions, in terms of development of species composition over time and canopy structure build-up, we consider the four stages a successional series (WERGER et al. 2002).

There was a clear shift in stand structure and species composition along the early successional series. Species composition between the stages clearly overlapped, but with longer protection from grazing the vegetation grew taller and several inherently shorter species disappeared, while several taller-growing species got established. In the tallest stage, the *Miscanthus*-stands, several tall-growing herbs, climbers, and even shrubs had established between the tall growing grasses and sedges, as well as a few inherently short species that commonly occur in shady undergrowth, though the biomass of these shade-tolerant species remained relatively small. In all four successional stages tiny seedlings of the forest trees had established and some seemed to survive and grow for more than one season.

Most conspicuous was the shift in dominance as the vegetation grew taller. While *Zoysia* overwhelmingly dominated the *Zoysia*- and *Hydrocotyle*-stands, it had strongly declined in the taller *Brachypodium*-stands and had disappeared from the very tall and dense *Miscanthus*-stands. *Brachypodium* was scarce and tiny in the *Zoysia*-stands, increased to sub-dominance in the *Brachypodium*-stands, but had virtually disappeared from the very tall *Miscanthus*-stands. *Hydrocotyle* showed a similar pattern, with its highest biomass in the *Hydrocotyle*-stands. Some *Miscanthus* seedlings were found in the grazing lawn but this species does not tolerate heavy grazing; under protection from grazing, however, it soon reached full dominance.

A number of narrow-leaved ground rosette-plants, such as *Liriope minor*, *Carex humilis* and *Calamagrostis epigeios,* profitted from the cessation of grazing as they managed to stretch their leaves to surprising lengths in dense and tall growing vegetation (Tab. 1). Other species were limited in the maximum leaf height they could reach when the vegetation grew taller, e. g. *Agrostis clavata, Zoysia japonica, Hydrocotyle maritima, Luzula capitata,* and particularly so *Viola obtusa* and *Gnaphalium japonicum* (which reached 5 cm only).

Using the equations given above we calculated the light capture characteristics of all species in all stands. The light extinction coefficients (k) in the stages were around 0.50 and thus normal for grassland vegetation types. In all stands light capture increased with the aboveground biomass of the species and in each stand there was a clear hierarchy of dominant, usually taller, species with a relatively large biomass and large leaf area, capturing most of the incoming light, and subordinate species with much smaller biomass and leaf area values and capturing a much smaller proportion of the incoming light. Thus, this pattern was not very different from that of the Dutch swampy grassland.

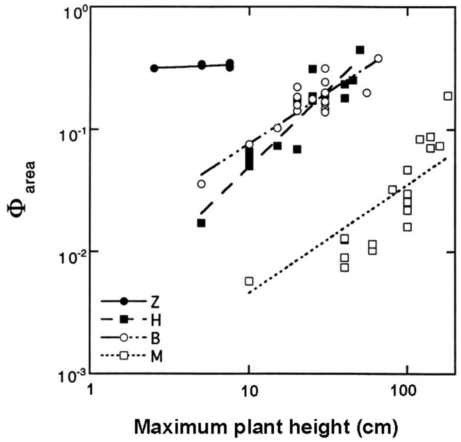
In the *Zoysia*-stands, where the canopy was very shallow and most leaves appeared to be well illuminated, variation in Φ_{area} between species was obviously small (Fig. 9), but Φ_{mass} differed considerably between species (Tab. 1, Fig. 10). This indicated that some species use considerably more biomass than others to harvest the same amount of light. In the other, taller-growing stands, which developed a steadily deeper shade lower in the canopy, light availability did play an important role in organizing the canopy: variation in Φ_{area} between species was larger (Fig. 9) and Φ_{area} and total leaf area were positively related, as also found in other studies (Hirose & Werger 1995, Anten & Hirose 1999). Particularly the increase of Φ_{area} with plant height was steep, showing that in tall and dense stands small differences in plant stature may have strong effects on plant performance (Fig. 9). In fact, it was shown in monospecific stands that initial size hierarchies are difficult to reverse (Schmitt et al. 1986, Weiner & Thomas 1986, Wilson 1988, Nagashima et al. 1995, Anten & Werger 1996, Anten & Hirose 1998, Hikosaka et al. 1999).

Tab. 1: Values of plant height (cm) and light absorbed per aboveground mass, Φ_{mass} (x 10 000); for species that occur in more than one stand type. The canopy height of the stand types is also indicated.

Stand type	*Zoysia*		*Hydrocotyle*		*Brachypodium*		*Miscanthus*	
Stand height (cm)	7.5		40		65		180	
	plant leaf height (cm)	Φ_{mass}	plant leaf height (cm)	Φ_{mass}	plant leaf height (cm)	Φ_{mass}	plant leaf height (cm)	Φ_{mass}
Galium pogonanthum	2.5	39.10	25	25.38				
Gnaphalium japonicum	2.5	72.61	5	0.40				
Luzula capitata	2.5	41.18	20	9.99				
Viola obtusa	2.5	58.20	10	5.31				
Carex japonica	5	42.59					100	2.59
Festuca rubra	7.5	23.20	40	16.21	55	11.89		
Hydrocotyle maritima	2.5	49.29	25	24.68	20	9.77		
Liriope minor	5	19.86	25	14.17	30	10.11		
Zoysia japonica	7.5	34.14	30	17.29	30	12.66		
Agrostis clavata	7.5	19.44			30	14.95		
Brachypodium sylvaticum	2.5	49.87	40	24.11	35	26.55		
Carex humulis			40	23.85	55	14.43	60	1.14
Calamagrostis epigeios					30	8.18	140	3.42
Miscanthus sinensis					65	21.20	180	10.48

As in the Dutch grassland, species differed in their mass use efficiencies (Φ_{mass} values). In three of the stages there was no relation between Φ_{mass} and total aboveground mass of the species; however, in the *Miscanthus*-stands there was a significant positive relation between Φ_{mass} and total aboveground mass of the species. Interestingly, however, when comparing at the same plant mass, shoots in the *Miscanthus*-stands had significantly lower Φ_{mass} values than shoots in the other stands (Fig. 10). In the *Miscanthus*-stands, the tallest species had about the highest light harvesting efficiency, reached the top of the canopy and contributed most to the biomass of the stand (Tab. 1). In the other, earlier-successional stages, however, the tallest-growing species were not necessarily the most efficient in terms of biomass use efficiency for light harvesting.

Highest efficiencies were found in some ground rosette species in the shortest vegetation type (e. g. *Viola obtusa, Gnaphalium japonicum*, Tab. 1), similar as in the Dutch swampy grassland.



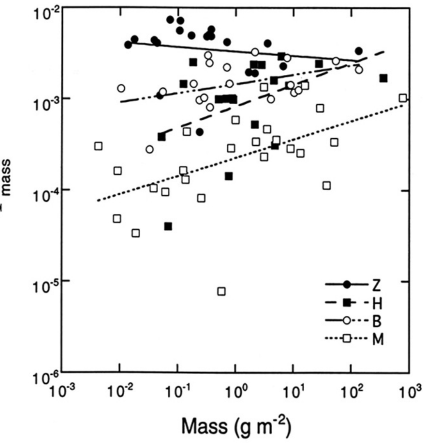


Fig. 9 (l): Relationship between light absorbed per area, Φ_{area}, and maximum plant height for 4 successional stages at Kinkazan, Japan. Z = *Zoysia*-stands, H = *Hydrocotyle*-stands, B = *Brachypodium* stands, M = *Miscanthus*-stands.

Fig. 10 (r): Relationship between light absorbed per aboveground mass, Φ_{mass}, and aboveground biomass for 4 successional stages at Kinkazan, Japan. Stages as in Fig. 9. Only the correlation for the *Miscanthus*-stands is significant ($p<0.01$).

In the taller vegetation, the trailing *Galium pogonanthum*, the creeping *Hydrocotyle maritima* which can extend its slender petioles to lift its leaf blades higher in the canopy (cf. LEEFLANG et al. 1998), and the long-leaved ground rosette plants *Brachypodium sylvaticum* and *Carex humilis* also reached relatively high efficiencies (Tab. 1). This shows that these species possess architectural characteristics that allowed them to position some of their leaf area higher in the better-lit parts of the vegetation canopy, with relatively moderate expenditure of biomass investment.

In the very tall *Miscanthus*-stands the high efficiencies were realized by an herbaceous climber, some tall herbs, and *Miscanthus* (WERGER et al. 2002; besides *Miscanthus* not in Tab. 1). These species managed to position their leaves high in the top of the vegetation canopy, where they captured a lot of light and therefore could assimilate sufficient biomass to maintain their top position. The tall herbs and *Miscanthus* did so by investing in robust stems and/or long, sturdy leaves. The climber used the neighbouring plants for support and therefore did not heavily in invest in support tissue (stems). In fact herbaceous climbers realize a considerable larger stem height per unit of stem biomass (DEN DUBBELDEN 1994, DEN DUBBELDEN & OOSTERBEEK 1995).

A shade-tolerant, short species of the undergrowth in the tall *Miscanthus*-vegetation, also realized a relatively high efficiency. This efficiency and the physiological traits of its shade-tolerance enabled it to persist low in the dark canopy.

In general, species that occurred in more than one stand type used more biomass to harvest the same amount of light as succession progressed, since they grew taller in the taller vegetation canopies and thus declined in their light harvesting efficiencies. This decline in Φ_{mass} values partly resulted from a shift in biomass investment pattern towards more support tissue, but it was more strongly caused by height growth limitations: the taller-growing species overtopped the stature-limited species and confined them to deeper parts of the canopy where there is less light available. This pattern was clearly shown by *Zoysia japonica, Hydrocotyle maritima, Carex humilis, Liriope minor, Festuca rubra, Viola obtusa*, etc. (Tab. 1).

In the *Miscanthus*-stands we classified the species in 'early successional' species (which also occurred in the earlier successional stands) and 'later successional' species (which first appeared in the *Miscanthus*-stands). Comparing the plants at the same height, we found that the 'early successional' species tended to have lower Φ_{mass} values than the 'later successional' species and the 'later successional' species tended to reach greater heights. The exception to this were a few 'later successional', low, shade-tolerant undergrowth species which also had relatively low efficiencies. The 'early successional' species also had significantly thicker leaves than the 'later successional' species, which contributes to explain their lower Φ_{mass} values. The biomass expenditure for light harvesting of the 'later successional' species was therefore more efficient and their relative growth rates may be potentially higher (cf. KÜPPERS 1985).

6 Grazing pressure and plant architecture

So far we showed that several plant traits affected a plant's performance and determined its position and success in the vegetation canopy, or its exclusion from the vegetation in this early successional series. In our explanation we emphasized three traits: the plant's pattern of biomass partitioning and its plasticity therein, the plant's architecture, and the plant's ability to survive as a shade-tolerant subordinate in the light-limited undergrowth. The plant's pattern of biomass partitioning and the plant's architecture relate directly to the height a plant can reach in a vegetation canopy relative to its neighbouring plants. And this relative height position in the vegetation canopy strongly contributed to explain the success of the species in this early successional series. But two conspicuous features in this early successional series remain to be explained. They concern the performance of the two dominant species in the series, *Zoysia japonica*, which totally dominated the earliest two stages, and *Miscanthus sinensis*, which completely dominated the later two stages. Why could *Zoysia* not also dominate the later two stages? And why failed *Miscanthus* to dominate also the two earliest stages?

The answers lie in the constraints of their architectures in combination with the absence or presence of the grazing pressure by the sika deer. It is not the grazing preference of the deer: both *Zoysia* and *Miscanthus* are eaten (TAKATSUKI 1980). *Miscanthus* also was not necessarily more efficient in light harvesting than *Zoysia*. *Miscanthus* took over because it can grow taller, while *Zoysia* could not. *Zoysia* is an inherently small plant that can only grow a very limited number of internodes from which leaves emerge before producing a terminal inflorescence. In the grazing lawn the internodes were extremely short, usually just 0.1 mm long, and in the taller stands these internodes could increase more than ten fold in length but nevertheless stayed short to relative to most other species. The result was that *Zoysia* could not reach more than 30 cm in height. In the grazing lawn *Zoysia* did so well because it could make itself very small with its extremely short internodes, its nearly horizontal leaves, and its robust buds and stems that apparently were well resistant to the deer's tread. In the *Hydrocotyle*-stands *Zoysia* grew up to its maximum of 30 cm. This was sufficient to still position its leaves high up in the canopy of those stands, and thus *Zoysia* maintained a high light capture. But it was its maximum height, and *Zoysia* could not match the stature of still taller species in the *Brachypodium*-stands, e. g. *Festuca rubra* and *Miscanthus sinensis* (Tab. 1). As the vegetation grew taller, *Zoysia* could not grow to the top and thus got stuck low in the vegetation. Consequently, its light capture became strongly reduced and, since it is not a shade-tolerant species, was not able to survive as a subordinate species in the light-limited undergrowth and got extinct: It had yellow, dead leaves along its basal stem parts in the *Hydrocotyle*- and *Brachypodium*-stands, and it had completely disappeared from the tall *Miscanthus*-stands.

And why did *Miscanthus* not dominate, and in fact was even scarce, in the grazing lawn? Also a result of a constraint of its architecture: it cannot grow short, and as a consequence it does not survive heavy grazing. *Miscanthus* could only grow long internodes of 8 to 14 cm before producing the terminal inflorescence. With 15 or more internodes it could reach a leaf height of more than 2.5 m in full growth and reach the highest position in the canopy. But *Miscanthus* could not grow short internodes, nor horizontal leaves. Thus, *Miscanthus* perpetually loses meristems under heavy grazing and cannot replace its lost leaves sufficiently fast. Once grazing was excluded, however, *Miscanthus* plants could rapidly outgrow other species and overtop these. They captured much light, grew fast, and gained dominance.

This is not a steady state situation, however. Among the species that invaded and maintained themselves in these early successional stages there were some woody climbers and shrubs. It may be expected that within a few years precisely such woody climbers (*Akebia quinata*) and shrubs (*Rosa multiflora, Stephanandra incisa*) will manage to become dominant: they have the advantage of starting their leaf growth year after year at a higher level in the canopy because of their perennial woody stems. That will enable them to overtop the herbaceous species and pre-empt the available light for their own benefit. *Miscanthus* is not shade-tolerant, and when overshaded it will diminish in vigour and ultimately disappear from the vegetation. The vegetation by then has become a dense scrub with climbers and some shade-tolerant undergrowth species. It is virtually certain that succession still will proceed and that the scrub will develop in forest vegetation. In nearly all our samples we found small seedlings of tree species (*Abies firma, Carpinus tschonoskii, Cornus brachypoda, Zelkova serrata*). They run a high risk of dying off in the shady conditions deep inside the taller vegetation canopies. But some may be expected to persist and grow and gradually get more advantage of their ever increasing leaf height on their progressively taller stems. With time they will dominate the canopy and build the forest.

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