ORIGINAL PAPER

Canopy effects on vegetation caused by harvesting and regeneration treatments

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Abstract This paper reviews the primary effects of canopy on understorey vegetation to provide insight into the management of the canopy space to benefit tree regeneration. Site conditions, like nutrient and water availability, overstorey conditions, e.g. tree species, and canopy density, are important determinants of ground vegetation. An investigation of canopy effects is concerned about how the canopy trees modify site conditions. As canopy density may be deliberately modified during regeneration treatments, the effect of canopy density on individual species in the herbaceous layer and tree regeneration is important. This autecological perspective focuses on the successional traits of species to help understand species differences in fecundity, survival, density and growth. From a synecological perspective, the importance of successional traits for the outcome of competition between species arising from differences in canopy densities is highlighted. This review shows that moderately dense canopies may favour tree regeneration over aggressive shade-intolerant graminoids or forbs. This is particularly true for shade-tolerant and intermediate shade-tolerant tree species. To better understand and utilise this phenomenon, research should try to identify and isolate different canopy effects.

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Introduction

The majority of vegetation management research in forests is concerned with the use of chemical or mechanical measures, or prescribed burning for regulating competition between shrubs, grasses, herbs, ferns and mosses, on one hand, and forest tree species regeneration on the other (Wagner 1993). Field experiments are often designed to investigate measures to restrict competing vegetation. Foresters rely on scientific research developing such measures for application in the field, e.g. on former agricultural land or on clearcuts. However, scientific research conducted at sites influenced by old trees has long shown that the composition and vitality of competing species under a tree canopy differs markedly from those in open field conditions (Lüpke 1982; Hannerz and Hånell 1997). Many species with high vitality in open fields loose much of their competitive ability under canopy conditions. Due to this shift in competitive ability in general, tree regeneration can be established under a canopy, thereby benefiting from the reduction in the vitality of competing vegetation and, as a result, simplifying vegetation management measures. Even so, the vitality of seedlings and saplings of tree species under a canopy may also be lower than in open conditions (Kenk 1988; Kuuluvainen et al. 1993). Thus, to implement a strategy of indirect competition management by utilising canopy effects, more knowledge about species-specific interactions under various canopy situations is necessary.

Moreover, it has been shown that the outcome of competition between species is site dependent (Küßner et al.

2000). Consequently, detailed investigations are needed to analyse how the canopy affects species growing below it. If a study of canopy effects is to include any relevant change in environmental conditions relative to an open field due to the influence of forest stands, the effect of shading (Canham et al. 1994) and root competition (Coomes and Grubb 2000) come to mind immediately. However, on a given site, one single canopy effect will rarely influence ground vegetation and tree regeneration independently of other canopy effects. How do different canopy effects interact in a given situation in forests?

This review seeks to give some insights into simultaneous canopy effects on ground vegetation and on tree species regeneration. In the section on "Fundamentals about canopy effects", we present an overview (1) about the main canopy effects and (2) about primary determinants of ground vegetation in general. We then show (3) how individual ground species respond to canopy effects and (4) how canopy effects influence the competitive outcome between species.

In the applied research section, we discuss (5) whether forest management can benefit from canopy effects to reduce the competitiveness of unwanted species while keeping the vitality of desired tree species regeneration at an economically acceptable level.

Fundamentals about canopy effects

Definition of canopy effects

Canopy effects is defined here as any change in environmental conditions at the forest floor level brought about by the presence of forest canopy when compared to clearances. Brechtel (1962), Mitscherlich et al. (1967) and, more recently, Heithecker and Halpern (2006) have reported critical findings about the effects of different canopy densities on microclimate at the forest floor. From these publications, we know that the canopy can influence the quantity and quality of light available, air and soil temperature and soil moisture. Furthermore, Beatty (1984) showed effects of canopy species composition on soil temperature, depth of litter and the quantity of nitrogen and calcium available in the humus layer.

These changes are primarily caused by trees, e.g. by their leaves, roots, branches and main stem. Yet, the influence of the trees may also be modified by herbaceous and woody vegetation (Heithecker and Halpern 2006).

As a forest stand is an assembly of individual trees, the environmental changes caused by single trees also needs to be considered. This has led to the notion of zones of influence or ecological fields (Wu et al. 1985; Grimm and Railsback 2005) of single trees. Some efforts have been undertaken to identify the effects of individual trees on light (Canham et al. 1994), water (van Noordwijk et al. 1996) and nutrient availability (Finzi et al. 1998a). In some cases, these findings have resulted in ecological field models, e.g. of light availability (Wälder et al. 2009). Other ecological effects of single trees included in ecological field models relate to pollen (Degen et al. 1996; Shimatani et al. 2007), seed (Clark et al. 1998; Stoyan and Wagner 2001) and leaf litter dispersal (Ferrari and Sugita 1996) as well as fine root distribution (Ammer and Wagner 2002). Most of these effects are important determinants of forest dynamics in a broad sense. Moreover, other phenomena are also driven by the interaction of the above-mentioned canopy effects in forest ecosystems, e.g. humus layer morphology (Finzi et al. 1998b; Wälder et al. 2008) and ground vegetation species (Kühlmann et al. 2001). Harmer and Morgan (2007) documented significant effects of canopy cover and distance to parent tree on oak regeneration.

To facilitate forest stand regeneration, foresters can modify tree species composition and stand density by cutting. A description of the effect of the total canopy in modified stands may be regarded as a combination of single-tree effects. To model the effect of an entire stand based on ecological fields of single trees, the effects of single trees are added in most cases, e.g. in leaf litter (Staelens et al. 2003), but a multiplicative approach is appropriate when modelling single-tree effects on resources, e.g. in light penetration (Wälder et al. 2009).

Determination of vegetation: general remarks

In investigations of canopy effects on species number, composition and vitality etc. of the herbaceous layer in forest stands, the main determinants of this vegetation layer should be investigated first. The two factors that modify this vegetation layer most are site and forest stand.

Determination of vegetation by site

Forest sites support complex systems resulting from the interaction of all environmental factors. Site, a natural unit, is the function of the interaction between climate, topography, parent material and vegetation over a specific period of time (e.g. Attiwill and Leeper 1987). Site heterogeneity in forest landscapes frequently is higher than in other landscapes (O'Connell et al. 2000) due to the high proportion of rock outcrops, standing trees, fallen logs, variety of litter and various forms of biotic disturbance. Even within a defined area, site characteristics (micro-climatic conditions, soil heterogeneity, resources) are very diverse. This diversity in abiotic conditions causes diversity in the vegetation (Strandberg et al. 2005). The way plants cope

with resource changes, for example in soil nutrient concentrations or in water availability, is partly reflected in indicator values for plant species (Ellenberg 1996; Haeupler 2000), which can be deduced from soil type, and moisture and nutrient regime.

The concept of 'Potential Natural Vegetation' (PNV, *sensu* Tüxen 1956) is a tool for specifying sets of site conditions influencing plant growth and distribution for different vegetation types. PNV indicates the combination of species that would exist today under the prevailing environmental conditions in the absence of [past and present] anthropogenic influence when plant succession progresses to its final stage. The final stage of natural succession at each site depends upon climate and soil conditions. This means that specific soil and climate conditions determine the final vegetation stage, the climatic climax community and the so-called zonal vegetation (*sensu* Ellenberg 1988).

Current plant communities often comprise replacement communities resulting from anthropogenic activity. Examples of coniferous and deciduous afforestation show that, in addition to near-natural and natural forest communities, entirely man-made plantation forests (which Zerbe 2003 called 'Forste') can also be informal integrated into the Braun-Blanquet vegetation system.

Nutrients and humus The influence of nutrient availability on primary production and the structure and diversity of plant communities has been demonstrated in many communities along soil fertility and/or soil moisture gradients (Tilman and Wedin 1991; Briggs and Knapp 1995; Ebrecht and Schmidt 2003). Effects of soil resource limitations are more pronounced in soils with low fertility, where biomass production is low and plant communities are dominated by a smaller number of species using the most limiting resources more efficiently (Mamolos et al. 1995).

The main growth-limiting nutrients for plants in natural environments are nitrogen and phosphorus (Vitousek and Howarth 1991; Koerselman and Meuleman 1996; Hofmeister et al. 2002; Güsewell 2005). For this reason, studies on mineral nutrition have focused mainly on these nutrients.

The rate at which nutrients circulate within the forest ecosystems (Ovington 1965; Ponge 2003) influences humus form, which varies according to climate and parent rock (Baritz 2001), but also to canopy and vegetation (Beniamino et al. 1991; Aubert et al. 2004), stand age (Emmer and Sevink 1994; Fischer et al. 2002), management (Liski 1995; Vanmechelen et al. 1997) and fertilisation (Deleporte and Tillier 1999).

Like the plants themselves, organic matter, in terms of its distribution and various humus forms, can be regarded as an integrated indicator of functionality of soils (Fischer et al. 2002). Organic matter has been classified into three organic matter types diverging in morphology: the mull type which has very active fauna and microflora, mor type which does not and moder type which lies in between.

Water Apart from non-organic chemical elements and organic matter, soil productivity depends on water (Ernst 2004). Soil water availability influences primary productivity and species composition (1) directly, since water is required for plant establishment and growth and influences the length of the growing season during the summer, permitting more species to share the temporal niche, and (2) indirectly by limiting nutrient availability and modifying soil characteristics, such as organic matter (Buczko et al. 2002; Bens et al. 2007).

Additional factors In addition to water content, nutrient status, soil fertility and climate, other environmental factors play a minor role in influencing ground vegetation in most forest ecosystems. Yet, some additional factors do influence distribution, evenness and diversity of understorey plants in temperate forests, notably edaphic conditions (Gilbert and Lechowicz 2004; Hofmeister et al. 2009), human activity (Ebrecht and Schmidt 2003; Godefroid and Koedam 2004) or former land-use (Fraterrigo et al. 2006).

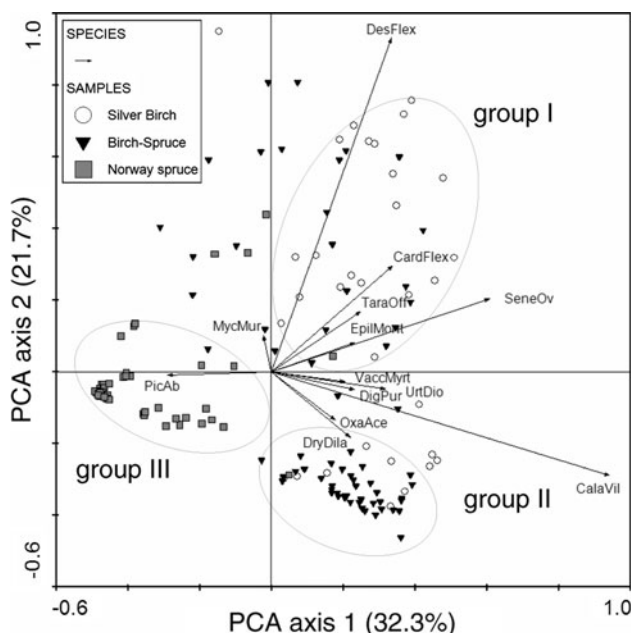### Determination of vegetation by stand, i.e. canopy effects

Ground vegetation is influenced by overstorey (species composition, structure and density) which, in turn, modifies site-specific resource availability (light transmittance, water competition and nutrient availability), other environmental factors (temperature extremes, wind speed) and additional factors such as litter fall.

The forest ground vegetation is rarely assumed to be the result of one specific ecological effect of the canopy alone. In fact, an interaction of various canopy effects is expected to determine vegetation characteristics. Seidling (2005) stressed that models predicting and explaining understorey floristic composition and its changes need to include a spectrum of parameters from different ecological domains. The mechanisms for different understorey vegetation responses to overstorey characteristics are complex, and careful attention is required to avoid overlooking these interactions when identifying the mechanisms involved.

Tree species The relationship between diversity and abundance of tree species within and between the canopy and understorey has been investigated (Beatty 1984; Jennings et al. 1999; Harrington et al. 2003; Aubert et al. 2004; Balandier et al. 2006; Hart and Chen 2006) and reviewed (Barbier et al. 2008) many times.

The effects of tree species in the canopy on the diversity and composition of understorey vegetation have often been discussed and comparisons made between conifer and hardwood forests. Based on a review of published data for understorey species richness, Barbier et al. (2008) found ten sites under a broadleaved forest canopy with greater species richness and four sites under a conifer canopy with higher species richness. There are indications that, in many cases, monospecific stands can be more favourable for biodiversity than mixed stands comprising two species. For instance, Schmidt and Weckesser (2001) have shown the influence of overstorey tree species composition on the diversity of ground vegetation in pure and mixed stands of Norway spruce and European beech. Their results showed clearly that species diversity was highest in pure Norway spruce stands and that canopy species composition affected species composition of the herbaceous layer, i.e. some understorey species were missing in European beech stands yet were abundant in Norway spruce stands. Likewise, Jobidon et al. (2004) found the proportion of Black spruce (*P. mariana* (Mill.) BSP.) mixed with broadleaved species to affect species richness of the herbaceous layer.

Figure 1 shows an example of the effect of the interaction between canopy tree species and resources on the

species composition of the herbaceous vegetation in a Norway spruce (*P. abies* (L.) Karst)—silver birch (*B. pendula* Roth) stand (Tischer 2009) based on a PCA. The PCA is one linear method attempting to relate species composition to hypothetical environmental gradients. The purpose of all ordination methods is to detect axes of the greatest variation in the community composition for a set of samples and to visualise the dissimilarity structure for the samples and species (Leps and Smilauer 2007).

The first group marked in the diagram is highly variable and includes predominantly samples taken near a single silver birch. In this group, the grass species *Deschampsia flexuosa* was more important than other species, as indicated by the long arrow. The second group is characterised by less variation and a different set of dominant vascular plants, e.g. *Calamagrostis villosa* and *Vaccinium myrtillus*. This group was almost exclusively sampled near a Norway spruce tree surrounded by silver birch. In the third group, Norway spruce saplings dominate the mixture and vegetation layer. The samples in this group were taken around a Norway spruce tree with no other tree species nearby.
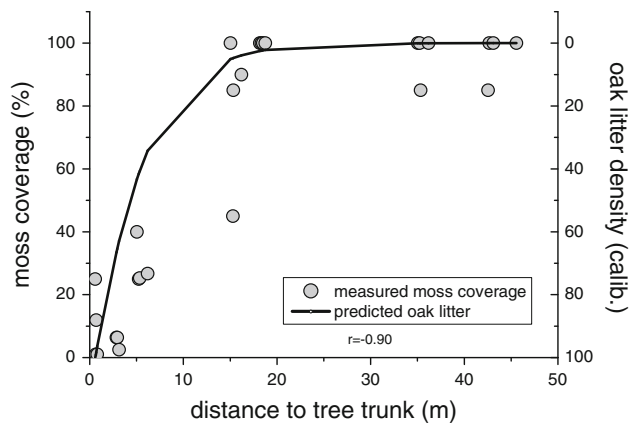
A separation of the samples into three groups is obvious. Therefore, effects of canopy species on species composition and coverage by different herbs are indicated. Wallrup et al. (2006) reported similar findings in boreal silver birch—Norway spruce mixtures.

In addition to diversity of herbaceous-layer, biomass may correlate positively with canopy species diversity. Mölder et al. (2008) stressed that productivity of the herbaceous layer could be promoted by increasing nutrient supply and base saturation. A higher proportion of beech in the canopy may reduce productivity of the herbaceous layer.

Litter may also affect tree species. The effect of litter fall on ground cover and species diversity may be positive or negative; while microclimate (e.g. humidity) may improve conditions for seed germination, seedlings cannot establish roots easily. Some litter removal experiments found litter thickness to inhibit understorey vegetation vitality or germination rates (Holderegger 1996; Augusto et al. 2003), whereas others found litter beneficial in seeding experiments (Ammer et al. 2002).

In Fig. 2, the example shows the relationship between moss cover and amount of broadleaf litter, suggesting that the amount of common oak (*Q. robur* L.) litter alone determines intensity of moss cover. Given the high acidotolerance of mosses, low moss coverage is probably due to the inability of mosses to survive the massive annual autumn leaf fall, as Ellenberg (1988) claimed. The nature of tamping effects by litter fall on understory vegetation seems to be non-linear and reversed above a definite amount of thickness (Suding and Goldberg 1999).

Fig. 1 Ordination-biplot of a Principal Component Analysis (CANOCO) for species of the herb layer (Tischer 2009). Each arrow denotes a single species of the herb layer. The samples are divided into three groups of canopy layer species (see legend). The longer a single arrow, the higher is the value (cover, individuals) of single species within the sampling locations around them. Smaller distance between *arrow* and *axis* represents a higher correlation between the two values. The first ordination axis explains 32.3%, the second axis 21.7% of the variance of species data

Fig. 2 Moss coverage and oak leaf amount on a poor sandy soil in a Scots pine (*P. sylvestris*) stand in relation to distance to a single pedunculate oak (*Q. petraea*) tree in that stand. Scale for oak litter density is inverted. Data of moss coverage (*circles*) are from Wehnert, unpublished. Oak litter amount data (*solid line*) are from a distance-dependent litter model (Lehmann 2007) and are calibrated to 100% at tree trunk

Canopy density When forest management deliberately designs regeneration measures in a stand, it generally follows the idea of assigning growing space (e.g. sensu Oliver and Larson 1996) to the regeneration that was previously occupied by one or several old trees. Seedlings can utilise this growing space, but it is also available to the remaining old trees and competing ground vegetation. In plant communities, growing space reflects the resource supply (Tilman 1982), and modifying canopy density can modify site-specific resource availability.

Relative light intensity (RLI) is used to determine growing space in many studies (Bolstad et al. 1990; Sonohat et al. 2004; Xiao et al. 2006; Arias et al. 2007). At the stand level, the size, shape, angle, orientation, arrangement and density of leaf layers can also be seen as critical crown parameters of single trees, tree groups (mixed tree species) or canopy structures affecting light availability. The parameters leaf area index (LAI, e.g. Küßner 1991) and gap light index (GLI, *sensu* Canham et al. 1990 and Dai 1996) are also used to quantify canopy and light conditions in forest understorey. However, it is clear that these parameters cannot be measured in isolation (Harper 1977).

Even though the shade tolerance of understorey species varies (Ellenberg classified vascular species along a gradient of nine indicator values), light is commonly considered to be the most limiting parameter for ground vegetation coverage, abundance, composition, height and species richness (Schmidt 2005; Barbier et al. 2008). However, changes in canopy density influences not only light regime; other microclimatic changes may occur such as air and soil temperature or humidity (Barkman 1992).

We know that ground vegetation is adapted to light regimes in stands, which have specific transmittance. Many European beech forest species have adapted to unfavourable light conditions (e.g. *Oxalis acetosella* L., *Luzula luzuloides* (Lam.) D. & Willm.), or complete their development cycles within 1 year, before the canopy is fully closed (geophytes in nutrient rich beech stands). Thus, the light factor in most beech forests has virtually no influence on species number in the ground vegetation (Härdtle et al. 2003).

Hofmeister et al. (2009) investigated the influence of light availability on species richness in the ground vegetation in oak-dominated forests in central Bohemia. They found positive correlations, with one exception.

In high light environments, graminoids are especially strong and effective competitors. The growth rates and belowground root density of these grass species increase markedly under better light conditions. Moreover, it is well known that graminoid species often have a competitive advantage when resource availability is high, including high light availability (Kull and Aan 1997). This feature allows them to colonise new soil volume efficiently, and rapidly take up available resources (Balandier et al. 2006).

In most ecological studies, radiation is traditionally quantified in terms of radiant energy and/or PAR (photosynthetically active radiation) irradiance. However, the quality of radiation, including its spectral composition within the canopy layer, is also important as it may influence physiology and the photosynthetic apparatus (Navrátil et al. 2007; Grant 1997). However, understanding whole plant photosynthesis is complicated due to the pronounced spatial PAR differences (Meir et al. 2002). The canopy reduces the total light intensity received by understorey vegetation and filters light rays selectively (Combes et al. 2000). Thus, in addition to the quantity of solar radiation, the quality (wavebands) may play a role for growth and competition within forest ecosystems as well. Changes in radiation quality, in terms of the ratio of red (RR) to far red radiation (FR), occur naturally in the forest canopy because the transmitted radiation and reflected radiation at the forest floor have lower ratios of red to far-red photons than the incident radiation at the forest canopy (Kozlowski et al. 1991). Although the influence of RR:RF ratio on the photosynthetic characteristics of plants is described in some studies as being limited (see Schmitt and Wulff 1993; Lee et al. 2000), some recent work shows that it may be more important than previously thought—especially in the context of interspecific competition (see section entitled "Competition between two species under varying canopy densities").

Leuchner et al. (2007) quantitatively compared light quality and light availability in a mature mixed Norway spruce–European beech forest over an entire vegetation

period in southern Germany. The red:far red ratios indicated a non-linear relationship between light availability and light quality. The relationship varied seasonally by vegetation/forest type and by meteorological conditions. Beech exhibits a higher variability in R:FR relationship than spruce. The results obtained facilitate the assessment of light quality from light availability measurements, and vice versa, under different types of mature mixed forest.

Heterogeneity is another important factor in light regimes, especially if direct light and diffuse light are partitioned. The photon flux density of direct and diffuse radiation is fundamentally different. The response of different plant species to particular combinations of these radiation components varies significantly (Larcher 2001). For example, the amount of diffuse and direct radiation varies within gaps, from the gap centre to the edge, and along N-S and E-W gradients (Canham et al. 1990; Wayne and Bazzaz 1993; Ritter et al. 2005). For this reason, scientists examining the influence of direct and diffuse relative radiation on certain measured parameters classify their plots into microsite types according to the prevailing combination of direct and diffuse radiation (Diaci 2002).

In addition to light, water is an essential resource for ground vegetation. Canopy density may affect soil water availability by changing (1) amount of non-intercepted water, (2) quantity of water absorbed by tree roots and (3) spatial distribution of water at trunk and crown. Water uptake by roots is species dependent and is modified by the specific morphology of the root system. Leuschner et al. (2001) were able to show the differences between distributions of fine roots, which cause a high interspecific competition with ground vegetation. For example, European beech has a denser fine root system than sessile oak or Scots pine. (Curt and Prévosto 2004). By high water absorption, fine roots in the upper soil horizons near the surface may limit ground vegetation vitality. Powell and Bork (2006) investigated the effect of the removal of aspen (*Populus tremula*) canopy on understorey vegetation, and Vincke et al. (2005) showed that understorey can sometimes take up more water than the overstorey trees.

In acidophytic beech and mixed beech–oak forests, there is a high positive and a negative correlation between the number of ground vegetation species and soil moisture, and light supply, respectively (Härdtle et al. 2003).

The mitigation of frost by canopies also deserves attention: as Agestam et al. (2003) show, beech regeneration suffers less from frost damage under dense or sparse shelter than in a clearcut. Frost mitigation for Norway spruce advance regeneration under dense shelterwood was very similar (Örlander and Karlsson 2000). The effect of canopies on frost occurrence can also be modelled (Blennow 1998).

In pure stands, i.e. stands with one overstorey species, canopy density is the factor which influences the

herbaceous layer most. Under a mixed species canopy, the understorey vegetation may be affected by (1) the dominant tree species, which determine the crown morphology, LAI and spatio-temporal variability in canopy openness (Falinski 1986; Collins and Picket 1987; Canham et al. 1990; Fischer and Bens 2002; Thomsen et al. 2005), or (2) the tree mixture (mixing degree or composition, Mölder and Schmidt 2007).

As, in forest management, cutting treatments are predominantly designed to create growing space for regeneration, the following discussion mainly addresses the effects of different canopy densities. However, the effect of species composition in the overstorey may be neglected in harvesting operations.

Canopy density effects on single species

Studies have been performed in which canopy density is adopted as an explanatory variable for different responses of target ground vegetation species to canopy effects (e.g. Tyler 1989; Moola and Mallik 1998). Both temporal (seasonal light availability—coniferous versus broadleaved tree species; Anderson and Loucks 1969) and spatial variability in canopy effects on ground vegetation are found (vertical gradient and horizontal differences, e.g. gaps or edges; Canham 1988; Collins and Battaglia 2008). According to Goldberg (1990), the vitality and growth responses of ground vegetation species and tree regeneration to different light conditions can be distinguished. Relationships between the explanatory variable and vitality variables may be linear (Modrý et al. 2004) or non-linear (Mountford et al. 2006). It seems that the nature of this relationship depends on the species and the explanatory variable, but often also on the scale chosen for the explanatory variable. Thus, for a better understanding of light effects caused by canopy closure or structure, it is necessary to distinguish between responses of ground cover species such as mosses, herbaceous plants and grasses (graminoids) and tree regeneration (seedlings and saplings). It is also necessary to differentiate between regeneration of light-demanding and shade-tolerant tree species (Brzeziecki and Kienast 1994).

Ground vegetation species

Vegetative growth   In the last 20 years, correlation analyses of light availability and vegetation cover or abundance were often carried out on plots (Bolte and Bilke 1998; Bisbee et al. 2001; Modrý et al. 2004; Denner 2007), resulting in estimations of small-scale spatial differences at the stand level (Cole and Weltzin 2005; Messaoud and Houle 2006). Species with high competition potential (Gaudio et al. 2008), e.g. genera like *Calamagrostis*,

Deschampsia, Epilobium, Vaccinium, Pteridium and *Rubus* (Tyler 1989; Pyšek 1993; Ricard and Messier 1996; Fischer and Bens 2002), were often the focus of these studies. A more detailed overview of 'recalcitrant' ground vegetation species was conducted by Royo and Carson (2006). The authors defined recalcitrant understorey plants as those with high resistance to displacement and which negatively affected other ground vegetation or tree species regeneration. Most of these studies were able to show positive linear relationships between light availability and cover of a single dominant species in the ground layer.

For light-demanding or early successional species, maximum light availability leads to maximum species cover (Anderson and Loucks 1969; Fischer and Bens 2002). For these species, light is the most important factor for them to dominate the forest ground cover (Wild et al. 2004). Thus, they are favoured by gaps, edges or openings in the canopy (Lieffers and Stadt 1994; Küßner 1999; Harrington 2006). However, ground vegetation includes different types of light-adapted plants (Ellenberg 1992; Fischer and Bens 2002; Lindh and Muir 2004). For example Gaudio et al. (2008) documented a strong linear increase in *Cytisus scoparius* (L.) link, with maximum cover of 70% in the 75% light transmittance class. In the same study, maximum cover of *Rubus idaeus* L. reached only 50%, and this occurred in lower class of approximately 45% light transmittance. Ricard and Messier (1996) found very low abundance of *Rubus idaeus* under light conditions below 10% PPFD (Photosynthetic Photon Flux Density). The same was documented by Lieffers and Stadt (1994), who found low abundance and cover of *Epilobium angustifolium* L. and *Calamagrostis canadensis* (Michx.) Beauv. in *Picea mariana* (Mill.) Britton stands when PAR transmittance was below 18%; yet above 25% PPFD, these species have a high presence. During 5 years of research in a 150-year-old pedunculate oak forest, Harmer and Morgan (2007) were able to show a continuous increase in *Rubus fruticosus* and *Pteridium aquilinum* cover after canopy cover was reduced. In the first year after cutting, these species covered 18% of the area, whereas, after 5 years, 80% of the stand was covered mainly by these species. However, Harrington (2006) concluded that there was no correlation between mean coverage of the two grass species *Anthaenantia villosa* and *Sporobolus junceus* and stand densities in *Pinus palustris* (Mill.) stands.

One of the rare examples of the use of light measurements to analyse bryophyte cover (e.g. *Sphagnum* sp.) was conducted by Bisbee et al. (2001) in black spruce forests in Canada. The cover of *Sphagnum* reached 10% on average and was positively correlated with PAR transmittance. However, with a LAI ($m^2\ m^{-2}$) of 4.2 in the overstorey, this moss was absent.

Analyses of total plant biomass production for different light-demanding species have shown positive relationships (linear or non-linear) between light availability and biomass of ground vegetation by area (Ricard and Messier 1996; Moola and Mallik 1998; Kotowski et al. 2001; Strengbom et al. 2004). Under closed canopy conditions in old Norway spruce forests, Pyšek (1991) measured a mean total biomass of 1,540 g/m^2 for *Calamagrostis villosa* (Chaix.) Gmel. compared to approximately 3,377 $g\ m^{-2}$ in clearings with full light availability.

Different light conditions modify growth ratios between leaves, shoots and roots, i.e. allocation features (Olff 1992; Edelkraut 2003). Harper (1977) described expansive root growth and restricted above-ground biomass development under high light exposition. The reverse was observed for canopy shadow effects (Kotowski et al. 2001; Sakamaki and Ino 2002). For *Vaccinium myrtilloides* (Michx.) in boreal mixed species stands, Moola and Mallik (1998) showed that increasing light availability resulted in increasing allocation of total biomass to leaf mass and decreasing allocation to stem mass. As with tree species regeneration, vertical light gradients change habits and silhouettes of herbaceous plants (Grime and Jeffrey 1965).

The ability to invest most energy into height development favours pioneer species in competition with climax species under suitable conditions. As suitable conditions, e.g. canopy gaps, are only available for a limited time, pioneer species respond with rapid height growth and capture open space rapidly (Yamamoto 2000).

Figure 3 shows the maximum height per plot of the pioneer *Epilobium angustifolium* in relation to light availability in gaps in a European beech stand. The dependence of height on light availability appears non-linear. Studies looking at height growth of ground vegetation species are rare compared to studies of regeneration; the one example available documented height growth for bramble (mean
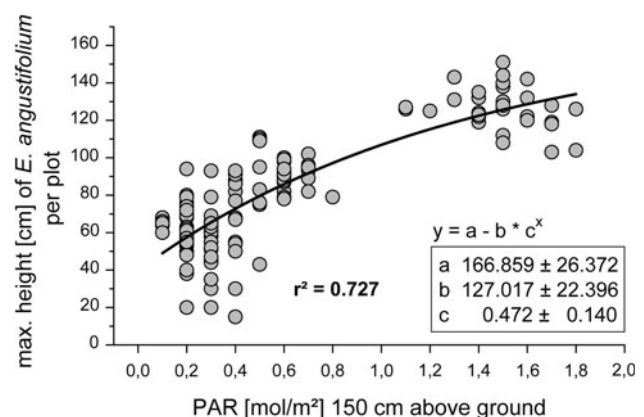
Fig. 3 Maximum height per plot of *Epilobium angustifolium* in relation to light availability in gaps in a beech-stand within the Solling Mountains; data from Fischer (unpublished)

height 64 cm) and bracken (mean height 85 cm) after cuttings in oak over 5 years (Harmer and Morgan 2007).

When plants are shaded by canopies (or by neighbours), they undergo a major reprogramming of their morphological development. Phytochromes are clearly involved in these responses to shade (Smith 2000; Ballaré 1999). The plants perceive a decrease in the ratio of red to far-red radiation, as described in the section on "Canopy density" above. This change in light quality serves as a warning for competition, triggering a series of responses known as the 'shade-avoidance syndrome' (Smith and Whitelam 1997). In response to shade, stems elongate and leaf expansion accelerates (Ballaré 1999). Many vegetative growth parameters of understorey vegetation may change in response to a change in light quality. These changes can be observed morphogenetic processes and plant architecture (Leicht and Silander 2006) or internode lengths, plant height, branching patterns, patterns of plant tissue allocation, leaf size, rooting ability and biomass (Newton et al. 1996; Stuefer and Huber 1998; Griffith and Sultan 2005).

Reproduction and survival rate Species maintenance in forest stands often depends on the ability of plants to flower and produce seeds (Thompson and Grime 1979; Hester et al. 1991). Some studies show strong, positive correlations between light availability and species fertility or number of inflorescences (Moola and Mallik 1998; Lindh and Muir 2004; Harrington 2006; Dorland and Willems 2006). Under closed canopy conditions, flowering is rare or impossible in some species (e.g. *Poa nemoralis* L. in Tyler 1989 and *V. myrtilloides* in Moola and Mallik 1998, *D. flexuosa* L. (Trin.) in Strengbom et al. 2004) because specific light and temperature requirements for inducing flower development are not met (Schopfer and Brennicke 2006). Dorland and Willems (2006) searched for the presence of flowering *Ophrys insectifera* L. em. L. (an endangered orchid species in many European countries) in forest stands in The Netherlands over a period of 4 years. A minimum RLI of 40–50% was necessary to guarantee good flowering conditions under a forest canopy. Generally, significant linear positive regressions were obtained between RLI and flowering of *O. insectifera*. From Pyšek (1991), we know flowering tiller densities for *C. villosa* under forest canopies lies between 25.4 ± 25.7 compared to 364.6 ± 276.7 per m^2 in clearings.

Shade tolerance in pioneer species is low for adult plants, and high rates of survival will only be achieved under open canopy conditions (Cole and Weltzin 2005). Harrington's (2006) studies in *Pinus palustris* stands provide an exception since no difference in survival rate of both grasses (*Anthaenantia villosa* and *Sporobolus junceus*) was found due to large differences in basal area of pine stands.

Regeneration of tree species

Hutchinson (1978) and Pianka and Horn (2005) described r- and K-specialists, which differ in their establishment strategies. Grime (2001) pointed out that the two groups also differed in their physiological metabolism, development and allocation response to different light conditions. The morphological, physiological and anatomical differences have been described comprehensively by Lyr et al. (1967), Harper (1977), and Larcher (2001).

For the management of forest tree species, Hutchinson's (1978) concept may be helpful to better understand traits of plant survival, density and growth of desirable tree species. This may be useful for predicting relevant development parameters for successful regeneration growth in relation to canopy density. Agestam et al. (2003) and Paquette et al. (2006) described an interaction triangle between shelterwood or canopy density, regeneration establishment and competition from ground vegetation. In accordance with Modrý et al. (2004), most studies of this interaction triangle in European forests appear to be restricted to European beech (*Fagus sylvatica*), pedunculate oak (*Quercus robur*) and sessile oak (*Quercus petraea*). Intensive research into other tree species (e.g. *Fraxinus* spp., *Acer* spp., *Tilia* spp., *Picea* spp.) may be seen as underrepresented. However, we have searched for a wider spectrum of tree species to find examples for the following topics.

Tree regeneration density Canopy density influences flowering and fruiting probability and intensity of most tree species (Karlsson 2000). Adult fruiting trees represent seed sources, and closeness to seed bearers may be decisive for regeneration density (Reader et al. 1995). The importance of distance to fruiting trees in determining seed presence and seedling densities is more pronounced in species with low seed dispersal ability, e.g. beech, than in pioneer species, e.g. birch. In general, a sound knowledge about seed dispersal of different species exists (Clark et al. 1998).

However, Janzen (1970) hypothesised that vicinity to conspecific adult trees would increase probability of seed occurrence and seedling mortality due to pathogens and herbivores. Some studies have justified this assumption (e.g. Packer and Clay 2000; Tomita et al. 2002). Shade tolerance of many tree species during the early stages of development is comparatively high (Beon and Bartsch 2003). In silvicultural management strategies, optimal canopy density and light regime become important for guaranteeing high seedling and sapling densities (Örlander and Karlsson 2000). Furthermore, seedling density research is concerned about suitable light conditions for competing ground vegetation, renewed canopy closure after low cuttings and damage caused by climatic effects, e.g. frost or drought (Agestam et al. 2003; Madsen and Hahn 2008;

Bílek et al. 2009). Most studies about light-demanding tree species have shown that seedling and sapling densities decreased with an increase in canopy density (Modrý et al. 2004; Dobrowolska 2008a). For Pedunculate oak (*Quercus robur*), Dobrowolska (2008a) found regeneration cover averaged between 60–86% under open, and 27–58% under dense canopy conditions (RLI < 16%).

Madsen and Larsen (1997) reported low sapling densities for European beech under a beech canopy with high LAI values (up to 5.8). Bílek et al. (2009), though not significant, described the same result. They subdivided the beech canopy into plots under (1) a canopy of parent trees, and (2) an open canopy. As a result, regeneration cover was higher under the open canopy compared to positions directly influenced by crown projection area. Overall, under a dense crown layer (RLI ≤ 11%), the lowest number of seedlings was observed. Studies by Agestam et al. (2003) and Modrý et al. (2004) pointed out that beech seedling density was low on clearcuts because of the lack of seed trees and the climatic damage, e.g. frost. There were no significant differences for beech regeneration densities under different canopy densities in the range from 12 to 49% (PAR) and 5.6–24.1% (RLI). Additionally, Modrý et al. (2004) emphasised that no canopy effect could be proven for *Picea* sp. and *Tilia* sp. regeneration, but density of *Fraxinus* sp. regeneration was negatively influenced by dense beech shelter.

Height growth rate Compared with quantitative research studies (density), height growth rate is often used as qualitative parameter to assess regeneration potential and vitality (Suner and Röhrig 1980; Welander and Ottosson 1998) as tree specific responses can be measured efficiently with minimal effort in the field (Ammer et al. 2004).

Non-linear, exponentially declining functions are commonly used in models predicting height and diameter growth in relation to RLI (e.g. Suzuki and Jacalne 1986; Pacala et al. 1994; Ammer 1996b; Schall 1998; Petritan et al. 2007; Wagner et al. 2009). Chrimes and Nilson (2005) have shown positively linear relationships between relative canopy openness and height increment at different regeneration stages (seedling, sapling, small tree) of the intermediate shade-tolerant species, Norway spruce. Lieffers and Stadt (1994) found a linear relationship in height growth until maximum growth was attained at 40% of transmitted light for *Picea glauca* (Moench) Voss seedlings, followed by decreasing height growth with a further increase in light availability. Dai (1996) found a non-linear relationship for height growth of *P. abies* regeneration to gap light index (GLI). Örlander and Karlsson (2000) studied height growth of *Picea abies* regeneration under different canopy density classes of 15, 27, 56, 75, 93 and about 100% RLI. They found the optimal canopy density

for mean height growth of Norway spruce regeneration to lie between the RLI classes 56 and 75%. These results can be considered characteristic for tree species with intermediate shade tolerance. Paquette et al. (2006) document another example of this kind of shade tolerance for *Quercus rubra* regeneration. Growth behaviour of this species was comparable to *Picea abies*, because maximal height growth could be observed under intermediate shelter conditions.

Height growth under low canopy densities differentiates pioneer tree species (light-demanding) from climax (shade-tolerant) tree species (Pacala et al. 1996). Regeneration of shade-tolerant species (e.g. *Fagus* sp., *Abies* sp., *Tilia* sp., *Taxus* sp.) utilises low light availability better due to anatomical and physiological adaptations (Mitamura et al. 2009), but has problems in further development (growth depression) when abrupt changes in light availability to 100% occur (Lyr et al. 1967). As we have seen, Agestam et al. (2003) found low regeneration densities for European beech on clearcuts. This was associated with low growth rates during the first years. However, after 6 years, European beech regeneration achieved the highest growth rates in open conditions and lowest under dense shelter. In the study by Madsen and Hahn (2008), beech seedlings showed negative responses in height growth during the first year after shelter cutting. Collet et al. (2001) described similar results in beech, showing constant height growth after canopy opening. Furthermore, annual height increment of beech seedlings under canopy (RLI 5.4–15.5%) and in canopy gaps (RLI 26.5–52.3%) ranged from 15–25 to 38–75 cm, respectively. Clearly, shade-tolerant tree species require more time to adapt to changes in light conditions than pioneer species. Different studies have shown positive responses in height growth for light-demanding tree species such as *Fraxinus* sp., *Quercus* sp., *Acer* sp., *Larix* sp., *Betula* sp. and *Ulmus* sp. with minimal time delays (Welander and Ottosson 1998; Modrý et al. 2004; Madsen and Hahn 2008). The early seedling growth of *Pinus densiflora* and three oak species (*Q. serrata, Q. mongolica, Q. variabilis*) was analysed under varying levels of light availability by Beon and Bartsch (2003). Combined with low moisture supply, a continuous increase in pine seedling shoot lengths was evident from 8 to 52% RLI whereas seedlings of oak species achieved their maximum height growth at lower light levels.

Emborg (1998) established a lower threshold of 3.5% RLI for height development of European beech compared to higher values for the intermediate shade-tolerant species, *Fraxinus excelsior* (Emborg 1998) and sycamore maple (Petritan et al. 2007), as well as in the light-demanding species, Scots pine (Dai 1996; Harrington 2006) and silver birch (Ericsson 1995). Welander and Ottosson (1998) established experiments to test adaptability of different tree

species under changing light conditions. RLI levels between 2 and 70% were chosen in this study. The authors stressed the relevance of temporal aspects in light availability caused by varying canopy density. During the first year of decreased shelter, European beech regeneration was distinguished by higher shoot development compared to *Quercus robur* seedling regeneration. In the second year, oak was characterised by an advanced shoot growth. When light availability decreased as a result of horizontal canopy growth, the shoot growth of both beech and oak regeneration decreased. Harmer and Morgan (2007) proved that the canopy of single trees in the overstorey affected height growth of oak seedlings. Oak regeneration under the vertical crown projection was significantly smaller in height than those outside the crown projection area.

Biomass and allocation   In studies from Lyr et al. (1963, 1964), detailed information about light responses of 2- and 3-year-old trees is available. *Quercus rubra* showed no changes in biomass production in different classes of relative light availability (class I.: 100–85%, class II.: 70–55%, class III.: 45–30%, IV.: = 15%). In comparison with this species, biomass decreases in *Betula pendula*, *Pinus sylvestris* and *Robina pseudacacia* were considerable between class III and IV. Biomass production of Douglas fir declined linearly in these light classes. In another study, pine seedlings produced between 6 and 10 times less biomass when exposed to only 8% RLI rather than 52% (Beon and Bartsch 2003). Studies from Burschel et al. (1985), Ammer (1996b) and Hunziker and Brang (2005) provide examples for biomass development in shade-tolerant tree species such as *Abies alba*. These authors have documented positive correlations between annual dry weight and canopy opening. Collet et al. (2002) refer to different studies, which have shown that beech seedlings adapted to dense canopy conditions with low light availability have low shoot–root and branch–stem ratios.

Allocation patterns in tree species regeneration follow the same physiological principles as were shown for ground vegetation earlier. High light availability caused by reduced canopy cover in the overstorey increases root biomass at the expense of biomass production of shoots and leaves, and vice versa (e.g. Burschel and Schmaltz 1965; Kramer and Kozlowski 1979). However, light-demanding and shade-tolerant species need to be distinguished (Thomasius 1988; Brzeziecki and Kienast 1994). Experiments by Lyr et al. (1967), Ericsson (1995) and Larcher (2001) show that light-demanding tree species like *Betula pendula*, *Pinus sylvestris*, *Fraxinus excelsior*, *Robina pseudacacia* and *Pinus nigra* experience a very steep decline in the root–shoot ratio if light availability decreases to any level, whereas for intermediate shade and shade-tolerant species (e.g. *Picea abies*, *Tilia cordata*,

Fagus sylvatica and *Abies alba*), root biomass production was favoured down to 35% RLI (Lyr et al. 1967). In the light experiments by Welander and Ottosson (1998), dry mass of all parameters increased significantly for beech with increasing light conditions. This was also found for number of leaves, leaf area and root–shoot ratio, yet no significant canopy effect on aboveground biomass was detected for oak seedlings in this study. However, root biomass, leaf area and number of leaves increased significantly with higher light availability in oak stands (Welander and Ottosson 1998). Grime and Jeffrey (1965), as well as Welander and Ottosson (1998), described the ability for tree species with heavy seeds to compensate the lack of light by seed sources during the first year of life.

Habit and morphology   At low light levels, trees will eventually show morphological adaptations to this environment (Lieffers et al. 1999; Roloff 2004). As the morphological changes may be indicators for tree development and future wood quality (Conrad 2005; Leonhardt and Wagner 2006), they may also be indicators for further management measures, e.g. canopy opening to enhance form and growth. The horizontal growth of terminal shoots, e.g. plagiotropy of *Fagus* sp. (Brown 1951), in low light may indicate poor quality. More detailed information about beech regeneration morphology and anatomy as a result of different canopy densities is provided by Collet et al. (2002). In their study, canopy effects influenced morphological parameters like length and width significantly. Banez et al. (1999) have reported bifurcation independence for different oak species under changing light conditions; yet mean branch length was high in RLI between 12 and 25%. Parent and Messier (1995) described morphological adaptations of balsam fir (*Abies balsamea*) along a shade gradient which was similar to those of Norway spruce (Greis and Kellomäki 1981). The characteristic 'shade habit' of *Abies alba* was described by Grassi et al. (2004) as a relationship between terminal shoot and branch lengths. Thus, the degree of apical dominance (ADR—apical dominance ratio) influenced by low or high light conditions was ascertained. Positive correlations between ADR and light availability were found. Dumais and Prévost (2008) adopted the same research approach for red spruce (*Picea rubens*) and balsam fir (*Abies balsamea*) with regard to different overstorey removal treatments. They documented the ratio of height growth (HG) to lateral growth (LG) for both tree species for 6 years after canopy change. After 6 years, the ratio was high for both tree species in the absence of canopy influence. However, when only 40% of the overstorey trees were removed, the HG/LG ratio was consistently low. Consequently, lateral growth increased disproportionately under low light conditions.

Further studies, including phenotypic plasticity and anatomical measurements, appear necessary for better understanding physiological responses of young plants (Collet et al. 2002).

Axelsson et al. (2006) investigated the morphological development of oak (*Quercus robur*) seedlings grown in different light qualities. The seedlings germinated in darkness for 3 weeks and were then given continuous light or short pulses of light. Stem elongation showed a high energy response, i.e. stem length increased only in continuous long wavelength far-red light but was not influenced by short pulses of red light or far-red light. Leaf expansion, however, was increased by short pulses of red light with a partial reversal of the effect by a subsequent pulse of far-red light.

The effects of shading levels, comparable to light quantity and quality below the canopy of a Norway spruce stand, on 1-year-old European beech and pendunculate oak were tested by Ammer (2003a) in a shade experiment. Beech seedlings showed a large decrease in height, diameter and dry mass of stems, branches, leaves and roots with decreasing light quantity. Neither growth rates nor total yield revealed a change in growth and biomass partitioning of beech as a result of slight changes in the red:far-red ratio. However, the relative growth rate of the oak main stem dry mass was considerably higher for seedlings in the shade treatment with a R-FR ratio lower than the control and the other shade treatment, whereas, when exposed to changed light quantity and quality, branch dry biomass decreased disproportionally, resulting in the lowest branch–stem ratio. The tallest oak seedlings occurred under the treatment with reduced light quantity and quality, whereas the control produced the shortest seedlings.

Further development of growth models should integrate the effect of light quality on growth, particularly for light-demanding species (Ammer 2003a; Ritchie 1997).

Survival In early seedling stages, moisture supply and nutrient reserves contained in the seeds (Fenner 2000; Silvertown and Charlesworth 2001) are important factors for successful germination and survival. Seed size in particular determines the survival of different tree species during the first year. Hence, seedlings of some light-demanding tree species such as oak may survive under low light conditions. However, after all nutrient reserves have been used, appropriate canopy density becomes essential for seedling survival.

It is common knowledge that the number of tree species that survive in light conditions below 2% of full daylight is small (Lyr et al. 1967; Madsen and Larsen 1997; Emborg 1998; Dobrowolska 2008b). Shade tolerance characteristics of tree species were determined by the minimum RLI value seedling required to survive in shade (Pacala et al. 1996).

Thresholds for tree species with low (10–12% RLI), intermediate (4–5% RLI) and high shade (1–3% RLI) tolerance (Lieffers and Stadt 1994; Banez et al. 1999; Örlander and Karlsson 2000; Collet et al. 2002; Petritan et al. 2007) may be found. Even so, pine seedlings were able to survive independent of the degree of light transmittance (Karlsson 2001; Harrington 2006). In addition, oak seedlings demonstrated no significant differences in mortality between gaps, edges and closed forest canopy (Collins and Battaglia 2008). This contradicts results from Pagès et al. (2003), who reported that shade had a negative influence on survival rate of *Picea* sp., *Abies* sp., *Acer* sp. and *Fagus* sp. in stands in the northern French Alps. According to experimental findings for height growth and biomass production, the optimal light level for maximal survival rates of shade-tolerant tree species varies between 100 and 2% RLI (Agestam et al. 2003). Furthermore, site quality, degree of canopy openness and dominant species in the overstorey of research plots may explain these opposite results. Once a minimum threshold of canopy openness is given, e.g. under pine on better soil, oak will have no difficulty surviving under a variety of canopy densities (Mosandl and Kleinert 1998). Above all, differences in survival ability are also influenced by differences in regeneration establishment (natural vs. artificial) and previous growth development (Collet et al. 2002; Agestam et al. 2003; Paquette et al. 2006). For older established plants, the probability of survival under unfavourable environmental conditions increases. Örlander and Karlsson (2000) have documented high survival rates for Norway spruce natural regeneration under a dense canopy when the plants had achieved shoot lengths over 20 cm. In this study, shelterwood densities with less than 74% RLI resulted in a 10% survival rate of small Norway spruce seedlings (shoot ≤ 20 cm) whereas plants greater than 50 cm in height experienced a 75% survival rate. Löf et al. (2007) found tree species-specific survival responses in underplantings of different tree species. In their model with light as single factor only for Norway maple (*Acer platanoides*), European ash (*Fraxinus excelsior*), pedunculate oak (*Quercus robur*) and Norway spruce (*Picea abies*), the influence of light on survival rate was significant; this was not so for wild cherry (*Prunus avium*) and lime (*Tilia cordata*). Experiments with artificial regeneration produced a lower sensitivity of the survival response to canopy effects than natural regeneration. Thus, Collet et al. (2002) and Paquette et al. (2006) found that the survival rate of planted tree species was independent of light availability. This may be due to protection and competition from overstorey trees overriding the relevance of light conditions (Royo and Carson 2006).

Furthermore, partially closed canopies may affect browsing behaviour and therefore there may also be an

indirect shelter effect on survival rates. As snow melts later on sheltered sites and seedlings are covered longer, plants on cleared areas are browsed more (Ammer 1996a). Schulze (1998) stressed the complex interdependencies between survival rates of natural regeneration, coverage and competition power of ground vegetation and browsing intensity by roe dear.

Finally, the establishment of seedling banks (*sensu* Silvertown and Doust 1997) represents a strategic adaptation to prevailing high canopy densities and is mostly observed in shade-tolerant species such as beech and hornbeam (Shibata and Nakashizuka 1995; Abe et al. 2005) and intermediate shade-tolerant species such as *Acer pseudoplatanus* (Ammer 2003b). This has also been reported for oak under pine canopies (Mosandl and Kleinert 1998) and for spruce in mixed mountain forests in Bavaria (Burschel et al. 1992).

Canopy density effects on multi-species performance

Canopy density effects on stand scale

Some broadcast treatment experiments have documented the impact of different harvest intensities on the herbaceous layer of forests. In mixed maple forests of southern Ontario, Burke et al. (2008) found a linear increase in diversity and herbaceous species richness with increasing harvest intensity 2–6 years after treatments. However, this occurred at the expense of forest specialist species.

A very similar result was obtained by Ammer (1996b) who found increasing herbaceous species richness and diversity in the Bavarian Alps with increasing RLI values 17 years after cutting treatments in mixed European beech-Norway spruce stands. However, the relationship between species number and RLI was non-linear, i.e. exponentially declining. Consequently, the highest gain in species numbers with increasing RLI values was reached at low light levels between 10 and 20% RLI, whereas the gain in species richness above 30% RLI was linear and more gradual.

In their work on the effects of harvest intensity on ground flora of upland mixed oak forests, Zenner et al. (2006) found a clear gradient in species richness and ground cover 3–4 years after cuttings with increasing harvest intensity, with the highest values in clearcuts. However, graminoids, annuals and biennials as well as woody vines benefited most in terms of relative cover. Although the highest diversity was reached in clearcuts in the three investigations mentioned above, in fertile Norway spruce peatland forests in Sweden, Hannerz and Hånell (1997) found a higher richness and diversity of vascular plant species under light shelter compared to clearcuts 7–8 years after harvest cuttings, where total cover of vascular plants was similar in the two treatments applied. These

authors suggested that, in clearcutting, the more light and nutrient-demanding species, i.e. early successional species, gain importance while late successional species lose coverage.

Harrington (2006) reviewed experiments in longleaf pine (*Pinus palustris* Mill.) ecosystems with a maximum herbaceous cover being attained in thinned rather than non-thinned treatments. Thinning also increased species diversity.

In all investigations mentioned, the aggregated cover of all ground layer species increased following any cutting treatment compared to pre-harvest conditions. However, while Bergstedt and Milberg (2001) found the gain in cover of single species to increase exponentially at very high harvest intensities, as did Zenner et al. (2006), for aggregated ground cover, Ammer (1996b) found aggregated ground cover declined exponentially with increasing RLI values. Expanding the idea of Bergstedt and Milberg (2001), we suggest that the different response functions of herbaceous layer cover to increasing degrees of canopy openness in different studies can be explained by the most limiting environmental factor on the sites. While on sites with poor nutrient availability or with unfavourable temperatures during the growing season, e.g. in boreal conditions, an exponential increase in cover with canopy openness seems likely, whereas under more temperate, nutrient rich conditions where light is the limiting growth factor, an exponential decline may be observed.

Besides documenting the general gain in diversity and species richness in the herbaceous layer by canopy opening, the abovementioned investigations also appear to show consistently a shift in competitiveness from early- to late-successional species depending on the intensity of treatment so long as mid- to late successional species dominate the overstorey, e.g. spruce (Hannerz and Hånell 1997; Weisberg et al. 2003), beech, maple (Ammer 1996b; Burke et al. 2008) or oak (Zenner et al. 2006). While the proportional cover of late successional species drops relative to undisturbed conditions in these ecosystems, the early successional species, not surprisingly, gain importance following disturbances, i.e. harvest cuttings (see also Roberts and Zhu 2002). This may be seen in absolute gains in coverage of those species. This finding led Burke et al. (2008) to caution against the reduction of forest-dependent specialist species by high harvest intensities.

Lüpke (1982) found graminoids dominating a clearcut on a moderately nutrient-rich site in Germany 4 years after cutting while in a shelterwood nearby herbs prevailed by far; a gap cut in this experiment gave intermediate values of coverage of both functional groups. However, Weisberg et al. (2003) and Cole and Weltzin (2005) reported examples based on specific species competitive relationships which contradict this general statement.

Canopy density effects at edges and in gaps

Small-scale treatments take advantage of the forest edge as a transition zone between two contrasting environments, i.e. closed forest and clearing, where values of canopy coverage, basal area (Chen et al. 1992) and light at recently-cut edges (Matlack and Litvaitis 1999; Drever and Lertzman 2003) may show transect-like features with largely moderate conditions. Research into forest edge environments has been summarised by e.g. Matlack and Litvaitis (1999), particularly with regard to forest specialist species. Edges may therefore pose some threats to these species. As edge influence within a forest may also result in higher animal species numbers (Matlack and Litvaitis 1999) or in enriched tree seedling mixtures (Chen et al. 1992) compared to either closed forests or clearings, the competitiveness and coexistence of species in the moderate canopy openings represented by the forest edge deserve more attention. Aggregated retention at edges or edge cuttings—similar to strip shelterwood (*sensu* Nyland 2002)—may also be seen as an experimental opportunity to generate transects along a gradient of canopy openness from clearing to closed forests (e.g. Groot 1999). Gap experiments represent a similar approach to capture gradients of canopy openness on a small scale (Mosandl 1984).

Nelson and Halpern (2005) showed pronounced effects on species composition of green-tree retention in aggregates at edges. While early successional species gained importance with increasing distance to the edge of the clearcut, forest species kept their dominance in aggregates 1 ha in size. However, transition effects, extending about 15 m into the aggregate, and a few metres into the clearing from the edge were also observed. Hahn and Thomsen (2007) investigated the effects of gap formation on the herbaceous layer in a semi-natural forest dominated by European beech. They found higher diversity in gaps, and increasing proportional cover of light-, and soil nitrogen-demanding species with long-distance seed dispersal ability in the gaps. It should also be noted that the RLI threshold for these light-demanding species was 2% (Hahn and Thomsen 2007). Hanssen (2003) found a significantly higher coverage of *Deschampsia flexuosa* in 4-year-old gaps of 0.25 ha in southern Norway where the coverage of most other species declined compared to pre-harvest conditions. Figure 4 shows the percentage cover of all ground vegetation species—excluding tree species—in the first year after gap establishment in near-natural old European beech forest stands on acidic sandstone. In addition to the relative cover of species, herb species number, abundance and total ground vegetation biomass increase with light availability.

Taking forest stands consisting predominantly of shade-tolerant canopy species into consideration, one can
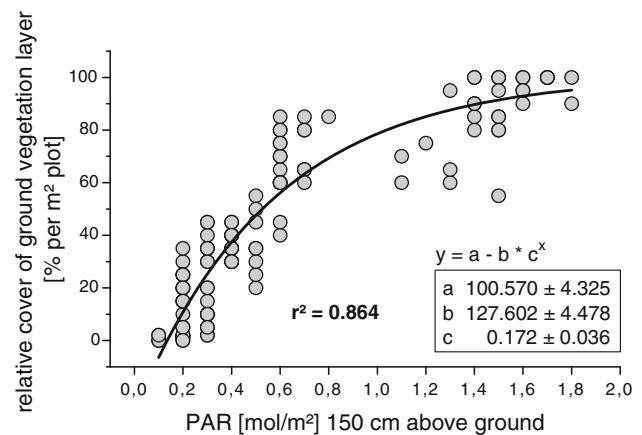
Fig. 4 Relative cover of ground vegetation layer in a beech-stand within the Solling Mountains in relation to light availability; data from Fischer (unpublished)

conclude, at this point, that there is evidence that the opening up of canopies, either by broadcast treatments or by group selection treatments, to create gaps shifts competitiveness in the herbaceous layer from late successional species to mid- or early successional ones. In temperate regions where fire is not a dominating disturbance factor, this corresponds to a shift towards light-, and nitrogen-demanding species. For Central European conditions, in particular, graminoids like *Calamagrostis epigejos, C. villosa, Carex brizoides, Deschampsia cespitosa, D. flexuosa, Molinia caerulea* must be considered. These species represent the major weed species in forests (see Röhrig et al. 2006, pp. 79). In many cases, invasive species benefit from canopy openings if they belong to the aforementioned guild of species.

In forests predominantly consisting of light-demanding species, e.g. pines, this shift has not been described yet. Rather, pyrophytic features may become much more important (Brockway et al. 2006) than factors associated with tolerance of shade.

Competition between two species under varying canopy densities

As well as the very general statement about the competitive shift between groups or groups of species of different successional status above, some investigations about canopy effects on relative vitality of two species in mixtures of ground vegetation have been published. Rice and Nagy (2000) found differences in the relative reproduction rate of two grasses under varying canopy densities in oak ecosystems. By focussing more on the vegetative growth of plants on a very fertile site under a European beech canopy, Mrotzek (1998) established a threshold of RLI, i.e. 7%, below which the proportion of *Mercurialis perennis* L. in

mixture was higher whereas above this threshold, *Urtica dioica* L. became dominant. Similarly, Bolte and Bilke (1998) analysed the competitive outcome between *D. flexuosa* and *C. epigejos* under a Scots pine (*P. sylvestris*) canopy. When RLI exceeded 32%, *C. epigejos* became dominant over and suppressed *D. flexuosa*. These findings show that a more or less sharp threshold of resource availability, i.e. RLI, may influence the competitive outcome between two species.

Therefore, height growth in early successional ground vegetation species such as *Rubus idaeus*, *Cytisus scoparius* and *Epilobium angustifolium* was analysed in different studies (Ricard and Messier 1996; Gaudio et al. 2008). For example, *R. idaeus* was dominant over *C. scoparius* in the mean transmittance class 45% and achieved plant heights of about 60 cm in stands of *Picea abies*. *R. idaeus* dominated light transmittance classes of about 75% with a mean plant height of 100 cm. Again, positive linear regressions between height of *R. idaeus* and light availability were evident (Ricard and Messier 1996), and the mean height of first-year vegetative stems (primocanes) reached 2 m at 40% RLI.

Application of canopy effects in silviculture taking tree regeneration into account

To this end, it may be assumed that the competitive outcome between species at the forest floor is dependent on the interaction between environmental conditions, the response of the species to those conditions, and the effect of the species on the environmental factors simultaneously. The complexity is enhanced when, for all species, all phases of the lifecycle relevant to the regeneration process are taken into account, i.e. in natural regeneration.
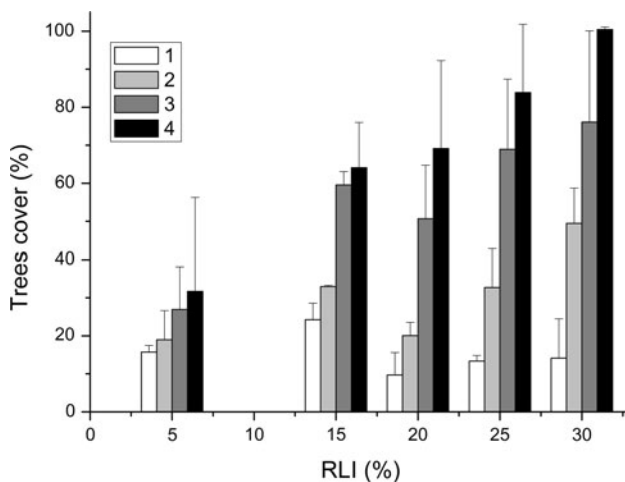
Consequently, one cannot expect to find a single environmental factor, e.g. canopy density, to be so important as to control solely competition at the forest floor. Nevertheless, in a meta-analysis of underplanting experiments, Paquette et al. (2006) found evidence that intermediate and light density shelterwoods were more favourable than clearcuts and control trials for height growth of the underplanted tree species. Similarly, the history of development of cutting systems (see Vanselow 1949) clearly demonstrates the use of different degrees of canopy closure to regulate the survival of tree regeneration. These systems utilise the spatial distribution of trees in the canopy layer to achieve the environmental conditions necessary for the survival of tree seedlings and saplings in the ground layer (Palik et al. 2003). Empirical evidence corroborates the importance of harvest intensities on tree species regeneration for the competitive outcome between early and late successional species. This fact is also reported in

silvicultural textbooks (e.g. Nyland 2002, pp. 242 for single-tree selection method; Röhrig et al. 2006, pp. 367 for Femelschlag).
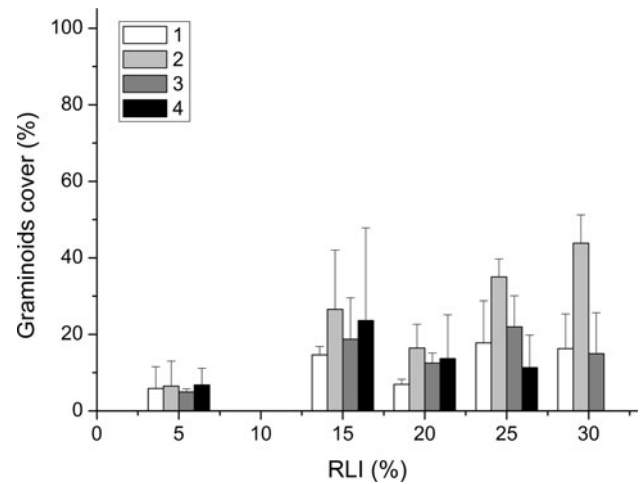
The complex long-term research studies by Mosandl (1991) and Ammer (1996b) in the European Alps have documented maximum regeneration densities after three different mast years for tree species in relation to RLI: for *Acer pseudoplatanus* and *Picea abies* at 18.4% RLI, for *Fagus sylvatica* at 10.2% RLI and for *Abies alba* at 8.2% RLI. It is of considerable importance that, in these complex studies, the highest tree regeneration densities are observed in low to moderate canopy densities but not under open canopy conditions. Maximum regeneration densities represent an indicator for differences in ecological niches of tree species in relation to canopy opening (Watt 1925; Hutchinson 1978). Below heterogeneous canopies (closed or sheltered canopy, small and large gaps), species-specific density differences create mosaic structures in regeneration at the stand level (Wagner 1999). This can also be seen in studies by Busing (1994) and Abé et al. (1995).

Furthermore, Lüpke (1998), reporting on the competitive outcome between sessile oak (*Q. petraea*) and European beech under varying harvest intensities, showed that the residual stand stocking must be very low and a threshold-like RLI value must exist for oak to have an advantage over beech. McClure et al. (2000) showed the importance of gaps for the regeneration success of yellow birch (*B. alleghaniensis*) in northern hardwoods in competition with shade-tolerant American beech (*F. grandifolia*) and sugar maple (*A. saccharum*). Canham (1990) and Yamamoto (2000) attributed the increasing densities of light-demanding tree species (e.g. birch) to favourable canopy conditions in gaps. Chen et al. (1992) found a gradient of distance to edges from clearcuts in the regeneration of Douglas-fir and shade tolerant pacific silver fir, with more silver fir regeneration in the forest remnants. Even less research is available about canopy effects on mixtures of an intact herbaceous layer and tree regeneration on one site. Böcker and Lochmann (1977) maintained the largest increment in height of naturally regenerated European beech seedlings occurred under beech shelterwood shade, i.e. an RLI of 15%, as graminoids have a high competitive potential when the canopy becomes more open. Under light shelter, grasses overtopped the beech seedlings, whereas, in shade, the beech seedlings grew more quickly than grasses even though beech shoot length increment was not high. Similar results were obtained for European beech by Lüpke (1987), who reported the largest height increment of planted beech after 8 years of moderate shading (RLI of 48%) compared to a nearby clearcut where the vitality of beech seedlings declined due to herbaceous competition and frost damage. Gray and Spies (1997) demonstrated that—compared to more open canopy

conditions—the highest survival rate of naturally regenerated Douglas fir seedlings in competition with vegetation cover of varying intensities occurred at the centre, and the southern edge of small gaps, i.e. canopy openings where the proportion of gap diameter to surrounding forest stand height was 0.4. Groot (1999) conducted an interesting edge-cut experiment with planted white spruce (*P. glauca*) in which he found the tallest spruce seedlings in the "no-herbicide" treatment after the second growing period near the edge, whereas, on the clearcut, the spruce seedlings were damaged by frost. Observing shade-tolerant white fir (*A. alba*) and European beech, Schmidt-Vogt (1972) found the highest survival rates under shade, i.e. RLI of 20%, compared to more open conditions, due to a more pronounced loss of ground vegetation vitality compared to the tree seedlings vitality. Likewise, regeneration density in gap studies of *Picea abies* seedlings was negatively correlated with light availability (Dai 1996). Ammer (1996b) found the highest sycamore maple seedlings (*A. pseudoplatanus*) under shade, i.e. RLI of 15%, compared to a shelterwood stand nearby which he attributed to competition from herbaceous vegetation under the light shelter, i.e. RLI of 25%. An example of a gap-cutting experiment in mixed deciduous forests in Central Europe on limestone is given in Fig. 5 (data from Wagner 1999). Beginning with less than 25% cover in the first growing season after cuttings, tree seedlings gained dominance within four vegetation periods, i.e. coverage of 100%, for RLI above 25% in gaps. The highest graminoid cover occurred in the second growing season (Fig. 6), but these were then overtaken by the trees while forb cover decreased

Fig. 6 Changes in relative cover of *graminoids* over time in relation to relative light intensity (*RLI*) in a gap experiment. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Bars* show succeeding vegetation periods after gap cutting; *error bars* show standard deviation
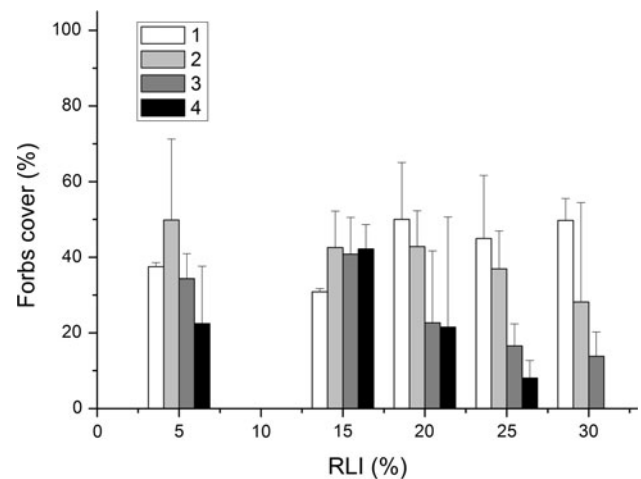
Fig. 7 Changes in relative cover of *forbs* over time in relation to relative light intensity (*RLI*) in a gap experiment. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Bars* show succeeding vegetation periods after gap cutting; *error bars* show standard deviation
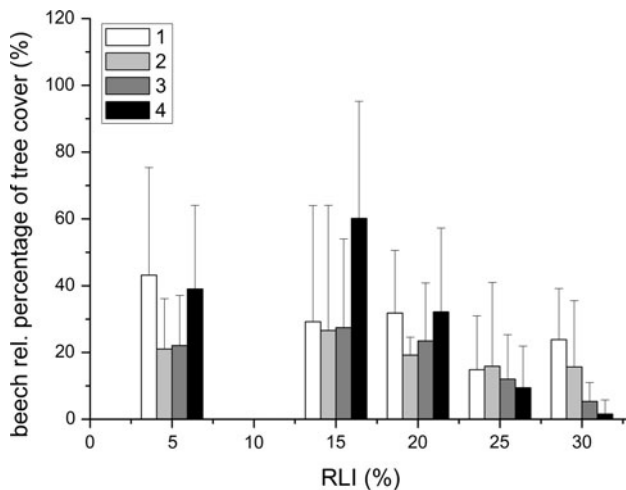

Fig. 5 Changes in relative cover of *tree seedlings* over time in relation to relative light intensity (*RLI*) in a gap experiment. Tree species are beech and ash predominantly. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Bars* show succeeding vegetation periods after gap cutting; *error bars* show standard deviation

continuously over time (Fig. 7). In moderate to low RLI values, i.e. less than 15%, neither trees nor the graminoids and forbs had established dominance after four growing seasons. However, trees were the only life form, which benefited in relative cover over time in all RLI conditions. In this investigation, tree species of different successional status were involved. In Fig. 8, it can be seen that the relative cover of late successional European beech declined with increasing light availability compared to other species. On this site, the intermediate shade-tolerant European

Fig. 8 Changes in relative cover of *beech* in percentage of total tree species cover over time in relation to relative light intensity (*RLI*) in a gap experiment. Prevailing tree species at RLI-classes higher than 15% is ash. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Bars* show succeeding vegetation periods after gap cutting; *error bars* show standard deviation

ash (*Fraxinus excelsior*) was favoured over shade-tolerant beech in particular at RLI values higher than 15% (compare to Fig. 5).

In an attempt to disentangle the various ecological factors affecting tree and ground vegetation growth, many experiments on the root competition from canopy trees have been carried out (overview in Coomes and Grubb 2000). As pointed out in their review, it is difficult to disentangle competition for light from competition for water without trenching experiments. However, York et al. (2003) conducted a gap experiment without trenching in Sierran mixed forests in California and found that Douglas fir and giant sequoia were sensitive to both drought and light shortage simultaneously. Dealing with herbaceous vegetation solely, Riegel et al. (1995) showed trenching effects on the biomass production; in a ponderosa pine (*P. ponderosa*) ecosystem, the effect of trenching was more pronounced than canopy reduction. Ammer (2000, 2002) demonstrated the importance of Norway spruce fine root competition for the growth of advance plantings of beech in a combined trenching and modelling experiment.

Silvicultural research has tried to define the circumstances under which tree regeneration benefits more than herbaceous vegetation from canopy effects. Lüpke and Hauskeller-Bullerjahn (2004) found different height growth responses of pedunculate oak and European beech to trenching of canopy trees roots, as well as to mechanical weeding. Weeding and trenching gave oak an advantage over beech when RLI exceeded 30% in 8-year-old planted seedlings. Trenching and weeding did not favour oak when RLI was below 30%. In the abovementioned gap

experiment on limestone, Wagner (1999) indicated additional effects of trenching on the competitive outcome differentiating forbs and trees. Although trees benefited from trenching, as shown by relative cover, across the entire light gradient after four growing periods (Fig. 9), the reverse was true in forbs (Fig. 10). Based on this finding, one can assume that, on this shallow limestone site, the combined effects of light and moisture supply determine the competitive outcome between forbs and trees. The more resources supplied—either by root trenching or by canopy opening or a combination of the two—the better the tree growth compared to forbs. Indeed, trenching may
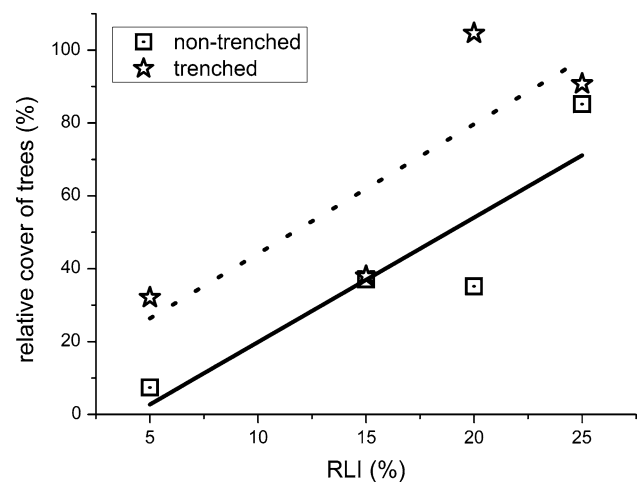
Fig. 9 Relative cover of tree regeneration in the 4th growing period after cutting in relation to relative light intensity (*RLI*) and trenching variants in a gap experiment. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Regression lines* are significant at $P < 0.1$
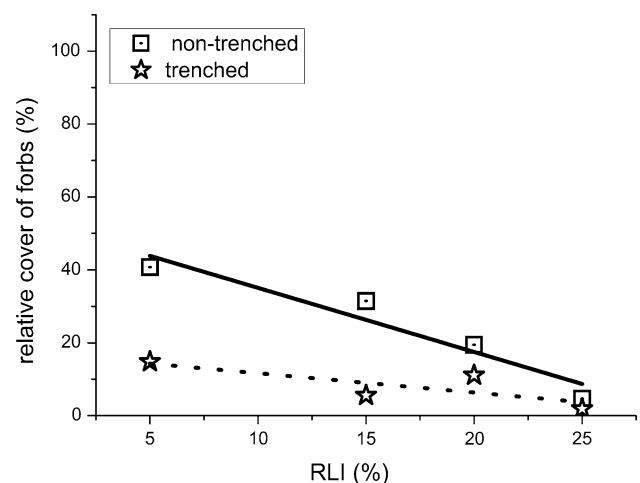
Fig. 10 Relative cover of forbs in the 4th growing period after cutting in relation to relative light intensity (*RLI*) and trenching variants in a gap experiment. Data from Wagner (1999); cover measured by photographic method represents the uppermost stratum of the herbaceous-layer. *Regression lines* are significant at $P < 0.05$

compensate for a light deficit to a certain degree, leading to the notion of a complementary resource relationship (*sensu* Tilman 1982).

The list of publications concerned with tree species regeneration in the presence of a competing herbaceous layer under varying canopy densities is short. However, the examples given show that, under particular circumstances, tree regeneration may develop best when canopy effects restrict the growth of herbaceous vegetation more than that of the tree seedlings. In doing so, the seedlings have a "relative" advantage over the herbaceous vegetation since seedling growth is lower under canopy than under more open canopy conditions with no herbaceous competition, e.g. due to herbicide application (Lüpke 1982; Groot 1999). The shade tolerance of tree seedlings is the main characteristic, which gives seedlings an advantage over the herbaceous vegetation. Most examples given above are concerned with European beech (Lüpke 1987; Ammer 1996b; Wagner 1999) or silver fir (Schmidt-Vogt 1972; Ammer 1996b), both shade-tolerant species. However, also intermediate shade-tolerant species like Douglas fir (Gray and Spies 1997), pedunculate oak (Lüpke 1982) or European ash (Wagner 1999) have been subjected to canopy opening treatments in experiments in which they gained an advantage over herbaceous vegetation.

Concluding remarks and research needs

The effects of forest stands on organisms at the forest floor are multiple and have been known for a long time (Ellenberg 1939). However, detailed analysis of habitat demands of those organisms with regard to canopy tree species and canopy closure are rare. Yet, there is emerging interest in animal research on this question, e.g. see Ziesche and Roth (2008) for soil-dwelling spiders and Fuller (2008) for carabid beetles.

In plant science and in tree regeneration in particular, the observations in most of the above mentioned studies were not explained by disentangling particular effects of canopy trees. It is, however, clear that tree species and stands density are important factors. This general statement may be qualified further by taking into account the canopy effects on resource availability, i.e. light, nutrients and water. By doing so, the general concept of competition for resources from Goldberg (1990) may be applied. Goldberg pointed out that the competitive strength of a species is due to both its ability to reduce the resource availability to neighbouring plants and its ability to withstand low levels of resource availability. From this approach, it is clear that research is needed to clarify the effect of herbaceous species on resource availability (see e.g. Landhäusser et al. 1996; Ter-Mikaelian et al. 1997; Shropshire et al. 2001). It

is, however, also clear that response functions are needed to assess the ecological amplitude of resource availability in which species maintain their growth vitality. Such functions for canopy density have been reported in the section "Canopy density effects on single species". More specific to tree regeneration, Davis et al. (1999) presented an "effect-response" scheme, which included herbaceous vegetation and oak seedlings as well as soil water, soil nitrogen and light availability as important components. To our best knowledge, no data are available that specify all the resource-based plant–plant interactions that need to be taken into account in a single complex canopy—tree seedling—herbaceous-layer system.

Although it does seem impossible to favour tree regeneration under specific conditions by appropriate manipulation of the overstorey canopy density, e.g. on rich soil under a pine canopy, to reduce graminoid competition, other questions are more open in this regard. Regeneration of intermediate shade-tolerant species and sites where the potential graminoid competition is high should be the focus of future research efforts. To improve future knowledge, integrated research incorporating knowledge from vegetation science, forest meteorology, soil science and regeneration ecology will be needed. Although this seems a difficult task, theoretical concepts exist for the input of empirical data, as it becomes available (see Davis et al. 1999). Research modules should include a definition of canopy effects as well as effect and resource availability response functions for tree seedlings and ground-layer species.

Today, ecological research about the effects of harvesting treatments on species and performance of the vegetation communities in the herbaceous layer is abundant.

These research activities are concerned about features of "old-growthness" (*sensu* Bauhus et al. 2009) or habitat continuity and often point to the fact that forest management may affect important ecological functions of forests, during harvest operations in particular. Yet, there is an urgent need for more research specifically into the niche partitioning between tree species seedlings and ground vegetation in relation to the nature and intensity of canopy cover (Lieffers et al. 1999). This review shows that, under specific circumstances and in some tree species, e.g. shade-tolerant and intermediate shade-tolerant species, habitat continuity may be beneficial for tree regeneration success as well. This may be due to the relative competitive advantage of shade-tolerant tree seedlings over herbaceous vegetation in general, and over graminoids in particular, under light to moderate canopy openings. At least under these circumstances, forest management may facilitate forest regeneration and habitat continuity simultaneously by designing specific, suitable harvesting measures.

However, these "specific" measures need to be defined appropriately.

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