Consequences of plant architecture and regrowth capacity for shoot competition among grasses

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CONSEQUENCES OF PLANT ARCHITECTURE AND REGROWTH CAPACITY FOR SHOOT COMPETITION AMONG GRASSES

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MESSERLI MARTIN
Dipl. Ing. Agr. ETH-Zurich

born 28 February 1965
citizen of Uetendorf (BE)

accepted on the recommendation of

PROF. DR. J. NÖSBERGER
examiner

PROF. DR. P. J. EDWARDS
co-examiner

1997
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CONSEQUENCES OF PLANT ARCHITECTURE, BIOMASS ALLOCATION AND REGROWTH CAPACITY FOR SHOOT COMPETITION

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<table>
<thead>
<tr>
<th>Abbreviation</th>
<th>Description</th>
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<tbody>
<tr>
<td>Cb</td>
<td>Competitive balance index</td>
</tr>
<tr>
<td>Csbh</td>
<td>Cb based on shoot yield</td>
</tr>
<tr>
<td>Cbsr</td>
<td>Cb based on stubble dw</td>
</tr>
<tr>
<td>Cbrw</td>
<td>Cb based on root dw</td>
</tr>
<tr>
<td>Cbt</td>
<td>Cb based on total plant dw</td>
</tr>
<tr>
<td>DW</td>
<td>Dry weight</td>
</tr>
<tr>
<td>I</td>
<td>PPFD in the canopy</td>
</tr>
<tr>
<td>Io</td>
<td>Reference PPFD above the canopy</td>
</tr>
<tr>
<td>LAR</td>
<td>Leaf area ratio (cm² mg⁻¹)</td>
</tr>
<tr>
<td>Li</td>
<td>Lithium</td>
</tr>
<tr>
<td>LN</td>
<td>Natural logarithm</td>
</tr>
<tr>
<td>LWR</td>
<td>Leaf weight ratio (mg mg⁻¹)</td>
</tr>
<tr>
<td>NAR</td>
<td>Net assimilation rate (mg cm² day⁻¹)</td>
</tr>
<tr>
<td>PPFD</td>
<td>Photosynthetic photon flux density (µmol m² s⁻¹)</td>
</tr>
<tr>
<td>Rb</td>
<td>Rubidium</td>
</tr>
<tr>
<td>RGR</td>
<td>Relative growth rate (mg mg⁻² day⁻¹)</td>
</tr>
<tr>
<td>RGRLA</td>
<td>Relative growth rate of leaf area (cm² cm⁻² day⁻¹)</td>
</tr>
<tr>
<td>RYT</td>
<td>Relative yield total</td>
</tr>
<tr>
<td>S.E.</td>
<td>Standard error</td>
</tr>
<tr>
<td>SAR</td>
<td>Specific absorption rate (ng mg⁻¹ day⁻¹)</td>
</tr>
<tr>
<td>SLA</td>
<td>Specific leaf area (cm² g⁻¹)</td>
</tr>
<tr>
<td>WSC</td>
<td>Water soluble carbohydrates</td>
</tr>
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<td>T</td>
<td>Transmission</td>
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GENERAL SUMMARY

The proportion of *Festuca pratensis* Huds. (Meadow fescue), a valuable component of meadows and pastures in upland regions, decreased drastically during the last century. *F. pratensis* is no longer persistent when grown with competitive companion grasses due to its low shoot competitive ability, probably as a result of an inherently low capacity for regrowth after defoliation.

Our objective was to assess regrowth of *F. pratensis* relative to *D. glomerata*, by means of growth analysis as well as the response of above-ground and below-ground plant traits to shoot competition and season. The goals were [1] to compare the regrowth capacity after defoliation of both species at non-limiting nutrient supply in a controlled environment, [2] to analyse the response of above-ground and below-ground plant traits of both grasses to shoot competition and season under field conditions, [3] to compare the seasonal variation of regrowth in intraspecific shoot competition and the whole plant response to regrowth after defoliation, [4] to study the effects of interspecific shoot competition on the whole plant and on regrowth after defoliation, and [5] to analyse the impact of root aphids on regrowth of *F. pratensis* after defoliation.

[1] The relative growth rate (RGR) of *F. pratensis* in hydroponics at non-limiting nutrient supply was lower than that of *D. glomerata* because dry weight did not increase during the first two days of regrowth. This was caused by a slower increase in leaf area ratio (LAR) due to a lower specific leaf area (SLA). *F. pratensis* was also less likely than *D. glomerata* to increase its SLA after defoliation and under low light intensity (20 μmol m⁻² s⁻¹). As well as differences in leaf traits, the lower RGR of *F. pratensis* was associated with 45% less area of the remaining green leaf sheaths after defoliation. Differences in the allocation of water soluble carbohydrates (WSC) to shoot sinks and in respiratory losses were not found.
Swards of *F. pratensis* and *D. glomerata* were grown in intraspecific and interspecific shoot competition in the field to study the effects of season and shoot competition on both species.

[2] *F. pratensis* was characterised by a higher biomass allocation to the roots and low root activity at soil depths of 0 to 0.12 m and 0.24 to 0.36 m, estimated from the uptake of rubidium and lithium. In contrast, *D. glomerata* allocated more biomass to the stubbles and had a higher total WSC content and root activity.

The shoot competitive ability of *F. pratensis* varied considerably with season, being high during reproductive growth and in autumn but much lower during summer.

The weak shoot competitive ability during summer was caused by a smaller proportion of leaf area in the upper canopy layers in interspecific shoot competition. *F. pratensis* responded to shading with reduced tillering, lower WSC accumulation in stubbles and roots, and a higher biomass allocation to harvested plant parts. In contrast, *D. glomerata* increased tillering, WSC accumulation, and biomass allocation to stubbles and roots in response to the greater availability of light in interspecific shoot competition.

[3] In intraspecific shoot competition *F. pratensis* had a higher RGR than *D. glomerata* during reproductive growth. This was the result of a faster increase in LAR in April, a higher NAR and, in 1994, a 50% higher proportion of reproductive tillers.

During the second regrowth in 1994, the low proportion of remaining vegetative tillers (25%) strongly reduced the refoliation and RGR of *F. pratensis* relative to *D. glomerata*. In contrast, during the summer of both years, RGR of both species, based on total plant dry weight, did not differ significantly.

*F. pratensis* generally showed a lower RGR of leaf area (RGRLA) and nutrient acquisition rate than *D. glomerata* for the first two weeks of regrowth. In contrast, LAR of both species increased similarly for one to two weeks, since *F. pratensis* had more residual leaf area and compensated for its generally lower SLA by a higher LWR. During the second half of regrowth, *D. glomerata* increased its LAR relative to *F. pratensis* due to its higher SLA and a higher biomass allocation to the shoot. As a result, *F. pratensis* in intraspecific shoot
competition reached an average leaf size of only 4.2 cm² in contrast to *D. glomerata* with an average leaf size of 10.8 cm².

[4] The lower RGR after the reproductive growth cycle in 1994 was an important reason for the lower shoot competitive ability of *F. pratensis*. In interspecific shoot competition, *F. pratensis* reached only a low relative leaf area density from the beginning of the growth cycle, which delayed drastically its restoration of WSC reserves. During summer, however, differences in leaf attributes and biomass allocation were more important limitations for shoot competitive ability of *F. pratensis*.

In response to interspecific shoot competition, *F. pratensis* increased its average leaf size (+25 %) mainly by increasing its leaf length and LAR. In contrast, the average leaf size (-25 %), leaf length, and LAR of *D. glomerata* were lower than in intraspecific shoot competition. Despite this contrasting response, *F. pratensis* was not able to compensate for its inherently lower SLA. Hence, *D. glomerata* still reached a higher total leaf area and considerably longer leaves in the mixtures and overtopped *F. pratensis* towards the end of the growth cycle.

In interspecific shoot competition, *F. pratensis* increased its shoot growth towards the end of the growth cycle, while neglecting root and stubble growth. In contrast, *D. glomerata* increased its root and stubble growth as compared to intraspecific shoot competition. This opposing response led initially to a similar competitive ability, based on shoot weight production, but to a fast, progressive decrease in competitive ability as expressed by the total dry weights of the plants.

[5] *F. pratensis* showed a high susceptibility to root aphids (*Geoica setulosa* Pass.). *D. glomerata*, the competitive counterpart, was not infested. Root aphids severely reduced the dry weight accumulation and restoration of WSC reserves of *F. pratensis* during regrowth after defoliation. The high susceptibility to root aphids may further reduce the persistence of *F. pratensis* in extensively managed permanent grasslands in mild regions.
ZUSAMMENFASSUNG


Kohlenhydrate (WSC) in den Spross oder in Respirationsverlusten traten nicht auf.

In Beständen mit *F. pratensis* - und *D. glomerata* in intra- und interspezifischer Sprosskonkurrenz wurden die Auswirkungen der Sprosskonkurrenz auf das Spross- und Wurzelwachstum untersucht.


Die Sprosskonkurrenzkraft von *F. pratensis* war starken saisonalen Veränderungen unterworfen; im generativen Aufwuchs und im Herbst war sie relativ hoch, im Sommer aber gering. Die geringe Sprosskonkurrenzkraft von *F. pratensis* im Sommer wurde durch eine geringere Blattfläche in den oberen Bestandeseschichten in interspezifischer Sprosskonkurrenz verursacht.


Während des zweiten Aufwuchs reduzierte der geringe Anteil nach dem Schnitt verbleibender vegetativer Triebe bei *F. pratensis* (25%) die Blattbildung und die RGR relativ zu *D. glomerata* aber stark. Im Sommer beider Jahre hingegen waren die Artunterschiede in der RGR, berechnet anhand der totalen Trockensubstanz, gering. Bei *F. pratensis* waren die RGRLA (RGR der Blattfläche) und Nährstoffaufnahmegeventerat wet der ersten ein bis zwei Wochen nach dem Schnitt geringer als bei *D. glomerata*. Die LAR beider Arten unterschied sich während
Zusammenfassung

der ersten Aufwuchshälfte aber nicht, da *F. pratensis* seine tiefere SLA mit einer höheren LWR kompensieren konnte. Während der zweiten Aufwuchshälfte hingegen nahm die LAR von *D. glomerata* verglichen mit *F. pratensis* dank der höheren SLA und einer höheren Biomass-Allokation zum Spross stark zu. Daher erreichte die durchschnittliche Blattgröße von *F. pratensis* am Ende des Aufwuchses nur gerade 4.2 cm², diejenige von *D. glomerata* aber 10.8 cm².


General Introduction

GENERAL INTRODUCTION

Plant competition is a process that occurs through the negative effects that individual plants have on resource availability to neighbouring individuals (Tremmel & Bazzaz 1993). Plants compete for different kinds of resources: water and nutrients below-ground and light, the main resource in the above-ground part of their environment. At low soil fertility, competition for soil resources may influence the growth of two competing pasture plants to a greater extent than competition for light (Tilman 1987; Wilson 1988; Wilson & Tilman 1993; Belcher et al. 1995). In contrast, competition for light (shoot competition) may have a greater influence on the composition of the vegetation at high soil fertility where canopies are sufficiently dense for an overlap of leaves to occur (Tilman 1987; Wilson & Tilman 1993; Carlen 1994).

In a dense canopy, species may differ slightly in height, inclination or orientation of foliage. In addition to this structural complexity, the leaf age distribution (Boller & Nösberger 1985) and the photosynthetic capacity of foliage elements vary within the canopy (Joggi, Hofer & Nösberger 1983) and among species (Beyschlag et al. 1990).

To be successful in competition for light, a plant must make as much use of the available resources as possible by means of pre-emption and/or compensation for the changes in resource availability by morphological and physiological plasticity (Tremmel & Bazzaz 1993). In order to pre-empt resources before they are consumed by neighbouring individuals, a rapid refoliation after defoliation is an important determinant of shoot competitive ability in intensively managed swards (Grime 1979). Species that are able to overtop others have numerous advantages in competition for light, mainly towards the end of the growth cycle when the canopy becomes denser (Caldwell 1987; Barnes et al. 1990; Holt 1995). Thus, shoot competition in pasture plants changes considerably during a growth cycle following defoliation.

Compensation processes for the changed resource availability in shoot competition affect growth, morphology, and biomass allocation of the whole plant (Givnish 1988). In turn, the changed plant architecture and plant physiology...
General Introduction

affects the ability to compete for above-ground and below-ground resources (Caldwell 1987; Holt 1995). If, for example, a plant has to allocate more biomass to the shoot in order to have better access to the limited resource light in response to shoot competition, this might well be at the expense of root and stubble growth or reserve accumulation which, in turn, might affect its competitive ability at a later stage. Hence, to understand the competition process, it is necessary to assess the effects of competition on resource availability of competing species as well as the response of above- and below-ground plant traits to these effects (Goldberg 1990). Therefore, experiments on shoot competition in pasture plant should include the whole plant because of the interdependence of the shoot and the root part of the plant.

Species are known to respond differently to seasonal changes in temperature (Jelmini & Nösberger 1978A) and light (Jelmini & Nösberger 1978B). Hence, the shoot competitive ability of different species and the parameters affecting shoot competition may change with season due, for example, to differences in the responses of plant architecture and regrowth after defoliation to changes in the environment. However, only a small number of field experiments on shoot competition among regularly defoliated pasture plants lasted long enough to study the seasonal changes in shoot competition (Remison & Snaydon 1980; Martin & Field 1984; Carlen 1994). Furthermore, these studies focused only on the response of above-ground attributes to shoot competition. None of them was suitable for studying the seasonal changes in the whole plant response to shoot competition or the changes in the response to shoot competition during regrowth.

The aim of the present study was to learn more about the plant traits that determine the outcome of competition in a regularly defoliated sward as well as about the processes limiting the shoot competitive ability of a species under rapid seasonal changes in the environment.

*Festuca pratensis* Huds. (Meadow fescue), a weak shoot competitor, and *Dactylis glomerata* (Orchard grass), a strong shoot competitor, provided a suitable model system for elucidating the effects of season and shoot competition on the whole plant and for assessing the consequences for morphological and physiological traits related to shoot competitive ability.
In the following paragraphs, certain parameters affecting shoot competition and regrowth in pasture plants are reviewed briefly. Thereafter, some of the studies of *F. pratensis* and *D. glomerata* will be examined and the objectives of this thesis will be defined.

### 1.1 Parameters affecting shoot competition

The ability of a plant to compete successfully for light in mixed species stands is determined both by its ability to intercept light and by its effectiveness in utilising this light in photosynthesis. Because of the rapid decline in PAR in dense canopies (Saeki 1963), most of the radiation, whether in monocultures or in mixed species swards, is intercepted in the uppermost part of the canopy (Joggi, Hofer & Nösberger 1983; Caldwell 1987). Indeed, the shoot competitive ability of a species in mixed stands is often affected more by differences in canopy structure than by differences in physiological characteristics of individual leaves (Wilson & Ludlow 1983; Barnes et al. 1988; Barnes et al. 1990; Ryel et al. 1990). Therefore, the ability of a plant to place foliage in the upper, well-lit canopy layers or to overtop another species is an important structural trait contributing to shoot competitive ability (Caldwell 1987; Barnes et al. 1990; Holt 1995).

In contrast, high photosynthetic capacity or features that allow a plant to fix more carbon than its competitors may be an advantage for species of similar height. In such circumstances, the inclination, orientation, and the total amount of foliage are also important in competition for light (Teughels et al. 1995). In species of similar height, plants intercepting more light at the top of the canopy with more horizontally oriented leaves will be more effective in shading neighbours (Caldwell 1987; Akey Jurik & Dekker 1990). Though, there are still many other factors, such as radiation characteristics, the density of the canopy, reflection, absorption, and transmission of the foliage, and the extent to which gaps in the foliage will allow sunflecks to penetrate that must be considered.

The availability of above-ground resources for the different species may change in interspecific shoot competition as compared to their availability in monocultures. Leaves absorb light in the blue and red regions and reflect or transmit
light in the green and far regions of the spectrum (Schmitt & Wulff 1993). Hence, if one species is shaded by another, light is enriched in far red wavelengths and has a lower red: far red (R:FR) ratio. Plants possess the ability to respond to the altered quantity and spectral quality of light induced by shading by morphological and physiological plasticity (Tremmel & Bazzaz 1993). A fast adaptation and a high adaptive potential of leaf attributes to changing environmental conditions can be important for the success of pasture plants in competition for light (Grime 1979; Rice & Bazzaz 1989; Olff 1992). Various responses to changes in light quantity and quality have been reported, a few of which are listed below (for a review see Caldwell 1987; Givnish 1988; Holt 1995). In temperate grasses, such responses may include an increase in leaf weight ratio and specific leaf area as well as increased leaf and stem elongation. In contrast, leaf width and thickness as well as the rate of leaf initiation, emergence, and expansion may be reduced in shaded plants. Increased biomass allocation to the shoots at the expense of biomass allocation to stubbles and roots or tillering are common responses to shade, too. The drain on the carbon and energy reserves of shaded plants may lead to reduced reserve accumulation or to starvation of the root system and its confinement to zones of nutrient depletion in the rhizosphere (Fitter & Hay 1981).

Plant species, however, vary considerably in their flexibility and capacity to respond to the altered quantity and spectral quality of light induced by shading (Olff 1992). Hence, the plasticity of, for example, leaf attributes of competing species has to be examined in order to understand their response to shoot competition.

1.2 Parameters affecting regrowth after defoliation

Rapid regrowth after defoliation as compared to neighbouring individuals may lead to considerable advantages in resource capturing in competition for light in an intensively managed sward (Grime 1979). Regrowth after defoliation of grasses depends on the amount and type of tissue removed in relation to plant development and the prevailing environment (Richards 1993). Depending on the season, the rate of regrowth after defoliation is related more to the content of
reserves (Shread 1973) and/or to the photosynthetic activity of the residual plant parts (Davies 1974; Davies 1988; Richards 1993). Water soluble carbohydrates (WSC), mainly stored in the tiller bases, are commonly considered to be an important source of carbon for regrowth after defoliation of forage grasses (e.g. Davies 1965; Smith 1973; Kigel 1980; Volenec 1985). Furthermore, regrowth after defoliation may be influenced by nitrogen reserves mobilised from tiller bases or roots (Ourry, Bigot & Boucaud 1989; Volenec, Ourry & Joern 1996; De Visser, Vianden & Schnyder 1997). In the field however, photosynthesis of remaining leaf area and leaf sheaths (Booysen & Nelson 1975; Richards & Caldwell 1985; Danckwerts 1993) or differences in quantity and activity of remaining meristems (Briske 1986; Davies 1988; Bassetti 1989; Richards 1993) are often more important for regrowth than differences in C and N reserves.

Species differ in their regrowth capacity due to inherent differences in the ability to re-establish foliage and to convert carbon and nutrients into new photosynthetic tissues and other plant structures. Under fertile conditions, species with a high maximal RGR are superior shoot competitors as compared to slower growing species (Grime & Hunt 1975; Poorter 1989). A high maximal RGR is usually associated with a high specific leaf area, a trait which gives the plant a high capacity to capture radiation without high matter costs (Poorter 1989; Lambers & Poorter 1992; Garnier 1992). Therefore, species with a high RGR may re-establish their photosynthetic tissue after defoliation faster than species which grow more slowly (Grime 1979). A low regrowth rate after defoliation of forage grasses, as a result of shading in the previous growth cycle, has also been reported (Booysen and Nelson 1975; Thomas & Davies 1978; Pierson et al 1990). Hence, species-specific differences in the regrowth rate of competing grasses may be the cause of a low shoot competitive ability as well as the consequence of shoot competition.

1.3 Decreased proportion of *F. pratensis*

In hilly regions, where alternatives for arable crops are rare, grassland for the milk and beef production are important sources of income for farmers. For a
General Introduction

number of recent decades, many of these permanent meadows and pastures have been managed more intensively. As a consequence, a shift in the floristic composition of grasslands has been observed. Species, adapted to a high input of animal manure and frequent defoliation or grazing increased and often dominate the communities. Especially in humid areas of hilly regions, problems associated with herbs increased, since most grasses have a low competitive ability under such conditions. At present, swards in these regions are often dominated by a high proportion of Umbelliferae, Ranunculaceae or Polygonaceae which lead to low quality of forage and a degenerated turf. Meadow fescue (Festuca pratensis Huds.), an excellent herbage grass in cooler regions, which is winterhardy and produces high quality forage, would be suitable for improving such degenerated grasslands.

More than one hundred years ago, Stebler and Schröter (1887) found that F. pratensis constituted 9 % to 36 % of the species in fertilised meadows and pastures at altitudes below 900 m. During the last century, the proportion of F. pratensis has continued to decline. Today, only a small proportion of F. pratensis is found in permanent grasslands and its persistence in sown grasslands is relatively low. Some of the direct causes of the low competitive ability of F. pratensis and its disappearance from permanent grasslands have not yet been identified.

It may be possible to breed cultivars of F. pratensis with a higher competitive ability. Introducing these cultivars into grasslands would be an ecological way of improving the quality of forage, the floristic stability, as well as the quality of the turf of pastures in higher and cooler regions. Before this can be achieved, it is necessary to understand the processes that determine the competitive ability of grassland species and the reasons for the low competitive ability of F. pratensis.

1.4 Low competitive ability of F. pratensis?

The intensification of grassland management is assumed to be one of the causes of the low competitive ability of F. pratensis compared to other grasses (Mott 1982). However, F. pratensis decreased relatively quickly almost independent of
defoliation frequency and fertilisation treatment in full competition with *D. glomerata*, which is often found with *F. pratensis* in permanent grasslands (Gügler 1993; Carlen 1994). Hence, there seem to be factors other than the intensity of management which limits the persistence of *F. pratensis* in our grasslands. Zimmermann (1995) analysed the importance of vegetative and generative propagation for the conservation of *F. pratensis* in a permanent grassland. The long-term survival of *F. pratensis* could not be ensured by vegetative propagation only. The generative propagation significantly enhanced the conservation of tillers of *F. pratensis* in the sward. The author concluded that *F. pratensis* must propagate by seed if it is to survive in permanent grasslands.

Malinowski (1995) tested the use of rhizomatous ecotypes or endophyte-infected ecotypes to improve the competitive ability of *F. pratensis*. The rhizomatous ecotypes had many morphological characteristics which were advantageous in competition with non-rhizomatous cultivars. The rhizomatous ecotypes were, however, highly susceptible to bacterial wilt and did not survive at low altitude. In growth chamber experiments, endophyte-infected ecotypes of *F. pratensis* were more competitive compared to *D. glomerata* than were non-infected cultivars, especially under water stress. These findings suggest that endophyte-infected ecotypes of *F. pratensis* may be more competitive in permanent grasslands. This might explain the high frequency of *F. pratensis* ecotypes infected with endophytes in permanent grasslands in Switzerland (Schmidt 1993).

In a field experiment, Carlen (1994) tested the importance of shoot and root competition for the persistence of *F. pratensis* relative to *D. glomerata*. The shoot competitive ability of *F. pratensis* progressively decreased during the two year experimental period. In contrast, the root competitive ability of *F. pratensis* was relatively high and changed with season. Carlen concluded that the weak overall competitive ability of *Festuca pratensis*, when grown with *D. glomerata* in very fertile soils, was mainly the result of a low shoot competitive ability. At the end of a vegetative growth cycle in July of the second year, the proportion of leaf area of *F. pratensis* in the upper layers of the canopy was only 3% (frequent defoliation) and 22% (infrequent defoliation). The low shoot competitive ability of *F. pratensis* was attributed to this low leaf area in the upper canopy layers.
1.5 Objectives

We hypothesised that an inherently low capacity for regrowth after defoliation, a slow rebuilding of leaf area, and/or a slower restoration of WSC reserves during regrowth may be the cause of the low shoot competitive ability of *F. pratensis*. The factors or the factorial combinations limiting regrowth and shoot competitive ability of *F. pratensis* could, however, change with season. Factors other than regrowth rate may be important at different season related, for example, to the species-specific response of leaf attributes and biomass allocation to the changes in environment or due to biotic stress factors. Further knowledge is needed about the seasonal change in regrowth rate and canopy structure of *F. pratensis* in comparison to a strong shoot competitor such as *D. glomerata* and its consequences for morphological and physiological traits related to shoot competitive ability.

The objectives of the present study were to analyse regrowth of *F. pratensis* relative to *D. glomerata* and the response of above-ground and below-ground plant attributes to season and shoot competition.

Our goals were [1] to compare the regrowth capacity after defoliation of both species at non-limiting nutrient supply in a controlled environment, [2] to analyse the response of above-ground and below-ground plant traits and canopy structure to shoot competition and season in the field, [3] to compare the seasonal variation in regrowth after defoliation in intraspecific shoot competition and the whole plant response to regrowth, [4] to study the effects of interspecific shoot competition in the whole plant and on regrowth after defoliation, and [5] to analyse the impact of root aphids on the regrowth of *F. pratensis* after defoliation.

It will be shown that shoot competition between *F. pratensis* and *D. glomerata* is a dynamic process changing with season and affecting above- and below-ground plant parts, that differences in leaf attributes and biomass allocation often affect shoot competition more than differences in regrowth rate, and that root aphids may strongly affect the regrowth of *F. pratensis* after defoliation.
PART I

REGROWTH CAPACITY OF FESTUCA PRATENSIS AND DACTYLIS GLOMERATA AFTER DEFOLIATION

1 SUMMARY

The regrowth capacity of *Festuca pratensis*, a weak competitor, as compared to *Dactylis glomerata*, a strong competitor, was analysed at non-limiting nutrient supply under hydroponic conditions.

*F. pratensis* had a lower regrowth capacity than *D. glomerata* due to a period with no increase in dry weight during the first two days of regrowth. This period was the result of a slower leaf area development after defoliation, caused by a slower increase in leaf area ratio (LAR) which could not be compensated by a higher net assimilation rate (NAR). After this initial phase, relative growth rate (RGR) of both species was similar; *F. pratensis* compensated a generally lower LAR by a higher NAR. The slower increase in LAR of *F. pratensis* was related to a lower and slower response of specific leaf area (SLA) to defoliation, while the leaf weight ratio (LWR) of both species increased at a similar rate. *F. pratensis* also showed a lower potential than *D. glomerata* to adapt its SLA to a low light intensity during regrowth.

As well as differences in leaf attributes, the lower RGR of *F. pratensis* was related to a lower rate of photosynthesis of remaining leaf sheaths (stubbles). This was due to a 45% lower stubble area, because all leaf area was removed by defoliation. Compared to differences in current photosynthesis, differences in water soluble carbohydrates (WSC), carbohydrate allocation to shoot sinks and respiratory losses were less important for the lower regrowth capacity of *F. pratensis*.

The competitive ability of *Festuca pratensis* in more fertile soils might be limited by an inherently low regrowth capacity after defoliation compared to *D. glomerata*. 
2 INTRODUCTION

*Festuca pratensis* Huds. (Meadow fescue) is an excellent, high quality forage grass in cooler regions. Because of its good winterhardiness and adaptation to humid conditions, it would be a suitable species under conditions unfavourable for ryegrass. However, *F. pratensis* is not very persistent when grown with competitive companion grasses nearly independent of defoliation frequency and fertilisation intensity. (Gügler 1993; Carlen 1994; Malinowski 1995). Carlen (1994) analysed the effects of shoot competition by *D. glomerata* (Orchard grass) relative to the effects of root competition on growth of *F. pratensis*. The field experiment showed that mainly a low shoot competitive ability related to a low leaf area proportion in the upper canopy layers limits the competitive ability of *F. pratensis* in fertile soils.

One of the major factors determining success in plant competition is the ability of a plant to extend leaves and roots in order to capture undepleted resources before they are consumed by neighbouring individuals (Grime 1979). Under fertile conditions species with a high maximal RGR are superior competitors as compared to slower growing species (Grime & Hunt 1975; Poorter 1989). A high maximal RGR is usually associated with a high leaf area ratio (Poorter 1989; Lambers & Poorter 1992; Garnier 1992), a trait which gives the plant a high capacity to capture radiation and is an advantage in competing for light. In regularly defoliated swards, a rapid replacement of photosynthetic tissue after defoliation or a fast and high adaptive potential of leaf attributes to changing environmental conditions can be important for competitive success (Grime 1979). Species often differ in their regrowth capacity due to inherent differences in their ability to promote regrowth, to re-establish foliage and to convert carbon and nutrients into new photosynthetic tissue and other plant structures.

The rate of regrowth at any time also depends on the quantity and quality of the remaining plant material (Davies 1988). In young vegetative forage grasses, grown in a controlled environment, regrowth is affected by the concurrent effects of residual photosynthetic tissue as well as the content of carbohydrate and nitrogen reserves. Water soluble carbohydrates (WSC), stored mainly in the tiller bases, are commonly thought to be an important carbon source for regrowth after
Regrowth at non-limiting nutrient supply

defoliation of forage grasses (Smith 1973; Davies 1988). Often however, concurrent photosynthesis of the remaining leaves and leaf sheaths affects regrowth more than differences in carbohydrate reserves (Richards & Caldwell 1985; Richards 1986; Danckwerts 1993).

We assume that the shoot competitive ability of *F. pratensis* is limited by an inherently low capacity for regrowth after defoliation, a slow rebuilding of leaf area and/or a slower restoration of carbohydrate reserves during regrowth. In the present experiment, we analysed the regrowth of *F. pratensis* relative to *D. glomerata* to compare their regrowth capacity at non-limiting nutrient supply and to evaluate parameters that might limit regrowth of *F. pratensis* in a permanent grassland.

Specific objectives of the experiment were: (1) to analyse the regrowth capacity after defoliation of both species at non-limiting nutrient supply under controlled environmental conditions, (2) to evaluate the adaptive potential of the SLA of both species during regrowth at low light conditions, (3) to estimate the efficiency in using reserve carbohydrates for regrowth, (4) to assess the impact of photosynthesis of remaining leaf sheaths on regrowth, and (5) to compare the relative contribution of reserve carbohydrates and concurrent photosynthesis of remaining leaf sheaths for regrowth of *F. pratensis*.

It will be shown that *F. pratensis* has a lower regrowth capacity than *D. glomerata* due to a slower increase in leaf area after defoliation and that photosynthesis of leaf sheaths affects regrowth more than the content of reserve carbohydrates.
3. MATERIALS AND METHODS

Regrowth of *F. pratensis* and *D. glomerata* after defoliation at non-limiting nutrient supply was analysed in three growth chamber experiments. In *experiment A* the regrowth capacity of the two species was compared. In *experiment B* the impact of photosynthesis of leaf sheaths on regrowth after defoliation was tested, and regrowth under low light conditions compared. In *experiment C* we focused on the relative impact of photosynthesis of leaf sheaths and water soluble carbohydrate reserves on regrowth after defoliation. Plant culture and environmental conditions were similar in all the experiments.

3.1 Plant culture

Seeds of *Festuca pratensis* Huds. cv. Predix (RAC, CH) and *Dactylis glomerata* L. cv. Baraula (Barenbrug, NL) were germinated for six days and grown in sand for 14 days. On day 20 after sowing, individual plants of each species with one tiller were transferred to containers (0.30x0.20x0.22 m). Eight plants per container were grown hydroponically on a complete nutrient solution with 2.5 mol m$^{-3}$ NH$_4$NO$_3$ and a pH of 5.5 (Hammer et al. 1978). The medium was continuously aerated and replaced every fifth day. Cylindrical plastic caps with a height of 3.5 cm above the root crown and a diameter of 4.2 cm were placed around the later stubble fraction of the plants. This approach helped to minimise species-specific differences in tiller angle.

On day 48 after sowing, all plants were defoliated to 35 mm above the root crown and the fresh weight of the harvested shoot part determined. The height of the plastic caps served as a reference for determining the defoliation height. The tillers were held upright, slightly pressed against the caps and defoliated horizontally by removing all the laminae, leaving only the leaf sheaths (here defined as stubble fraction). This method minimised differences in the initial stubble length and eliminated differences in the remaining leaf area. To reduce variance, the smallest and the largest 12.5 % of the plants of each species were eliminated, depending on the fresh weight of the harvested shoot parts. The remaining 75 %
of the total plant of each species were divided up into six replicates, depending on the fresh weight of the previously harvested shoot parts. After dividing the plants into these blocks, randomly selected plants from each block were harvested full destructively as reference plants, including the corresponding, previously harvested shoot of each plant. The rest of the plants was subjected to the regrowth treatments.

3.2 Environmental conditions

The experiments were carried out in growth chambers (PGV36, Conviron Instruments CO, Winnipeg, Canada) at 18/13 °C (day/night) temperatures, 70/80 % (day/night) relative humidity and a photoperiod of 16 h. Light was provided by cool-white fluorescent lamps (Silvania, CW/VHO, 215 W) and incandescent bulbs (100 W) at a ratio of 5:1. Irradiance and temperature increased stepwise in the morning and decreased stepwise in the evening over a period of 105 minutes. The photosynthetic photon flux density (PPFD) at the top of the pots was 500 μmol m⁻² s⁻¹ (measured with a quantum sensor, Li-185A, Li-Cor, Lincoln, NE, USA).

3.3 Treatments

3.3.1 Restriction of stubble photosynthesis

Immediately after defoliation and removing the remaining leaf area, the cylindrical plastic caps of 50 % of the plants were filled with approximately 1.5 g perlite and covered with 1-2 mm silica sand (0.1-0.5 mm). The perlite with the sand cover reduced the light intensity by 88 % at a stubble height of 33 mm and by 99 % at a stubble height of 28 mm. Thus, the photosynthesis of the remaining leaf sheaths (stubble photosynthesis) was restricted. The impact of stubble photosynthesis on regrowth after defoliation was assessed by comparing regrowth of plants with covered stubbles relative to reference plants. Preliminary experiments showed that tissue temperature of covered stubbles increased to 29 °C compared to 23.3 °C in reference plants. However, leaf growth and tillering
of both species was not influenced by the cover during the experimental period of seven days.

### 3.3.2 Variation in reserve carbohydrates

In *experiment C*, we focused on the impact of stubble photosynthesis relative to reserve carbohydrates on regrowth after defoliation. Plants of both species were grown in two growth chambers. Stubble photosynthesis was prevented as in the previous experiment. In addition, the pool of reserve carbohydrates in half of the plants was reduced by lowering the CO₂ concentration in one growth chamber for five days before defoliation. The plants were deprived of CO₂ by placing CO₂-absorbing filters containing soda lime pellets (MERCK, Darmstadt, D) into the ventilation system of the growth chamber. The CO₂ concentration was lowered to 20 ppm within 24 h, compared to an average of 450 ppm (ambient CO₂) in the control treatment. The use of CO₂ deprivation to lower the pool of carbohydrate reserves for regrowth has an advantage over other methods (e.g. increase of temperature, shading or placing into darkness) in that tissue temperature as well as light quantity and quality remain unchanged.

### 3.3.3 Regrowth under low light intensity

Plant sets of both species were transferred to a separate growth chamber immediately after defoliation to assess regrowth under low light intensity. Low light intensity (20 µmol m⁻² s⁻¹) was chosen instead of etiolated regrowth so as not to affect the diurnal rhythm of the plants. The day temperature was raised to 23°C to attain similar tissue temperatures as in the other experiments. The length of the photoperiod was 16 h similar to the other experiments.

### 3.4 Sampling and plant measurements

In *experiment A* plants were sequentially harvested fully destructively immediately after defoliation on day 0 and 1, 2, 3, 5, 7, 9, 12, 15, 18 and 21 days later. Twelve replicates (two plants per block) were harvested on day 0, 5, 7 and 21 after defoliation; six replicates (one plant per block) were harvested on all the
other dates. In the subsequent experiments six replicates (one plant per block) were harvested 0, 2, 3, 4 and 7 days after defoliation. At each harvest the tiller and leaf number per plant was counted. A tiller was included in the counts when its first emerged leaf was longer than 20 mm. Tiller length was estimated as the average of 8 to 10 randomly taken tillers. The plants were then defoliated as described above and separated into green leaf laminae, leaf sheaths, the stubble fraction and roots. The dry weight of these fractions was determined after drying at 65 °C for 48 h. Leaf area, leaf length and stubble area were measured with a photoelectric meter (Model Li-3000 A; Li-Cor Inc. Lincoln, NE, USA).

3.5 Analysis of water soluble carbohydrates

Approximately 10 mg of finely ground plant material were extracted in 1 cm³ of 80% (v/v) ethanol in water at 80 °C for 30 min. After centrifugation at 15000 x g for 15 min, the supernatant was retained and the pellet re-extracted with 1 cm³ of water in a sonicator at approximately 45 °C for 15 min. After centrifugation as above, the combined supernatants were used for carbohydrate extraction with the anthrone method (Dreywood 1946). The anthrone reagent was similar to that described by Deriaz (1961); 350 cm³ of water, 735 cm³ concentrated H₂SO₄ (p=1840 kg m⁻³), 10 g of thiourea and 865 mg of anthrone. Five cm³ of ice-cold anthrone reagent was added and the reaction mixture vigorously mixed. The tubes were arranged in racks of 60, covered with marbles and incubated in a water bath at 96.2 °C for 40 min. After 30 min at room temperature each sample was mixed, and the absorption at 625 nm was measured. All reactions were performed in duplicate.
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3.6 Data analysis

A completely randomised block design was used in all experiments. All investigations were performed with 6 to 12 replicates. For growth analysis the plant with the greatest and that with the least dry weight at each harvest were discarded (Poorter 1989). Growth analysis calculations were made according to the functional approach (Hunt 1982) using a PC edition (HP curves, Bristol, UK. Hunt & Parsons 1994) of the computer program of Hunt & Parsons (1974). Polynomials of varying degrees were fitted to Ln-transformed plant dry weight (W) and Ln-transformed leaf area (LA) against days after defoliation \( t_x \) by the least square method. Second order polynomials fit adequately to dW/dt of both species between \( t_2 \) and \( t_{21} \) in experiment A and between \( t_0 \) and \( t_7 \) in experiments B and C. Third order polynomials were used to fit dLA/dt between \( t_2 \) and \( t_{21} \) in experiment A and between \( t_2 \) and \( t_7 \) in experiments B and C. The following plant growth functions were used: relative growth rate (RGR=1/W x dW/dt), RGR of leaf area (RGRLA=1/LA x dLA/dt), net assimilation rate (NAR= 1/LA x dW/dt) and leaf area ratio (LAR=LA/W). All calculations not computed by the Hunt and Parsons computer program were done so with the SAS statistical package (Statistical Analyses System, Version 6.10, SAS Institute Inc., Cary, North Carolina, USA). Data were Ln-transformed before analysis of variance if variances were not normally distributed and were not homogeneous. Non-transformed data were used to calculate the specific leaf area (SLA= leaf area per leaf weight), the leaf weight ratio (LWR= leaf weight per total plant weight) and the harvest index (harvested shoot dw per remaining plant dw). Analysis of variance and standard error of the means (s.e.) were calculated according to the GLM procedure.
4 RESULTS

4.1 Analysis of regrowth after defoliation

The total plant dry weight and the tiller number of both species at defoliation, 48 days after sowing, were similar (Table 1). Shoot yield of *F. pratensis* was slightly higher compared to *D. glomerata*. The remaining plant dry weight after defoliation was slightly, but not significantly, higher in *D. glomerata*. However, the mean RGR of *F. pratensis* during the three weeks following defoliation was significantly lower (-7%). Hence, the regrowth rate of *F. pratensis* after defoliation was lower as compared to *D. glomerata*, despite similar initial dry weights right after defoliation.

Table 1: Tiller number per plant, total plant dry weight, and shoot yield of *Festuca pratensis* and *Dactylis glomerata* at defoliation as well as dry weight of remaining plant parts after defoliation and mean RGR during a regrowth period of 21 days. Means and standard errors (s.e.) of 10 replicates are shown.

<table>
<thead>
<tr>
<th>Parameters</th>
<th><em>F. pratensis</em></th>
<th><em>D. glomerata</em></th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Tiller number per plant</td>
<td>8.0</td>
<td>8.0</td>
<td>0.4</td>
</tr>
<tr>
<td>Total plant weight (mg dw per plant)</td>
<td>632</td>
<td>642</td>
<td>13.5</td>
</tr>
<tr>
<td>Shoot yield (mg dw per plant)</td>
<td>367</td>
<td>348</td>
<td>12.8</td>
</tr>
<tr>
<td>Remaining plant parts (mg dw per plant)</td>
<td>265</td>
<td>295</td>
<td>10.4</td>
</tr>
<tr>
<td>Mean RGR after defoliation (mg mg⁻¹ day⁻¹)</td>
<td>0.169</td>
<td>0.158</td>
<td>0.002</td>
</tr>
</tbody>
</table>

Regrowth was characterised by an initial period without dry weight gain followed by a period of exponential growth (Fig. 1). Ln-transformed total dry weight of *F. pratensis* remained at a constant level for two days (Fig. 1A). In contrast, the
Figure 1: Ln-transformed total dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), and leaf weight ratio (F) during regrowth after defoliation of *Festuca pratensis* (▲) and *Dactylis glomerata* (●). All remaining leaf area after defoliation was removed. For the estimation of RGR and NAR, second-order polynomials were fitted through the Ln-transformed dry weights from 2 to 21 days after defoliation in (A). Each point is the mean of four to ten replicates. Means as well as fitted values are shown in (A). Means are shown in (D & E). I represents the standard errors for the fitted values in (A, B, C & D) and the standard errors of the means in (E & F).
I Regrowth at non-limiting nutrient supply

period no increase in dry weight lasted only one day for *D. glomerata*. The longer period without dry weight accumulation led to a significantly lower dry weight of *F. pratensis* after three days of regrowth. After this initial period, the dry weight increase of both species was approximately similar.

To analyse the regrowth capacity of the two species after the initial period, functional growth analyses was used to estimate RGR and NAR during the period of exponential growth. Consequently, RGR and NAR calculations presented in Fig. 1 refer to the Ln-transformed dry weights during the period from day 2 to 21 after defoliation. RGR of both species decreased during regrowth (Fig. 1B). RGR of *F. pratensis* was slightly lower relative to *D. glomerata* from day 2 to 7 after defoliation but significantly higher at the end of regrowth. NAR of *F. pratensis* was, on average, 25 % higher as compared to *D. glomerata* (Fig. 1D). LAR of both species increased until five days after defoliation when it remained at a constant level (Fig. 1C). The increase in LAR after defoliation was faster in *D. glomerata* than in *F. pratensis*. Averaged over all harvests this difference caused a 22 % lower LAR of *F. pratensis* relative to *D. glomerata*. The faster re-establishment of LAR in *D. glomerata* was related to a considerably higher increase in SLA during the first three days after defoliation and a consistently higher SLA thereafter (Fig. 1E). In contrast, the LWR of *F. pratensis* was similar to *D. glomerata* until one week after defoliation and thereafter exceeded the LWR of *D. glomerata* (Fig. 1F).

The increase in shoot yield of *F. pratensis* was similar to *D. glomerata* during the whole regrowth period (Fig. 2A). Stubble growth of *F. pratensis* was curtailed for two days after defoliation, while stubble growth of *D. glomerata* continued after one day (Fig. 2B). The response of root growth of both species paralleled the response of stubble growth (Fig. 2C).
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Figure 2: Ln-transformed shoot yield (A), Ln-transformed stubble dw (B), Ln-transformed root dry weight (C), and harvest index (D) during regrowth after defoliation of Festuca pratensis (\(\nabla, \ldots\)) and Dactylis glomerata (\(\bullet, \ldots\)). After defoliation, all remaining leaf area was removed. Means of four to ten replicates and standard errors (I) are shown.

After this different initial response, the increase in stubble and root dry weight of both species was similar. However, the stubble and root dry weight of 
F. pratensis was consistently lower as compared to D. glomerata after three days of regrowth in consequence of the longer period without dry weight accumulation. Therefore, the constantly lower total dry weights of F. pratensis after the initial phase were mainly related to lower stubble and root dry weights. The differences in dry weight distribution of the two species led to a consistently higher harvest index of F. pratensis relative to D. glomerata after the first week of regrowth (Fig. 2D).
4.2 Changes in leaf and tiller attributes during regrowth

*F. pratensis* re-established its leaves after defoliation slower than *D. glomerata* (Fig. 3A). Differences in total leaf area were significant from the first day on during the whole regrowth period. The slower leaf growth of *F. pratensis* was partly related to a slightly lower RGRLA during the first five days of regrowth (Fig. 3B).

![Figure 3: Ln-transformed leaf area (A), relative growth rate of leaf area (B), tiller number per plant (C), and average tiller length (D) during regrowth after defoliation of *Festuca pratensis* (△,-) and *Dactylis glomerata* (●,—). After defoliation remaining leaf area was removed. Third-order polynomials were fitted through the Ln-transformed leaf area in (A). Each point is the mean of four to ten replicates. Means as well as fitted values are shown in (A). Means are shown in (C & D). I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C & D).]
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Tillering of *F. pratensis* was delayed after defoliation for approximately 12 days (Fig. 3C). After this period, the tiller number of *F. pratensis* increased four-fold from day 12 to 21 of regrowth. In contrast to *F. pratensis*, the delay in tillering in *D. glomerata* lasted only nine days. After this period, tiller number of *D. glomerata* strongly rose, leading to significantly more tillers from day 12 to 18 of regrowth. However, tiller number of both species was similar 21 days after defoliation, since tillering of *F. pratensis* from day 18 to 21 of regrowth was higher relative to *D. glomerata*.

In contrast to total leaf area and tiller number, tiller extension of *F. pratensis* was faster than that of *D. glomerata* (Fig. 3D). The average tiller length of *F. pratensis* was constantly higher during the whole regrowth period. Significant differences were found already one day after defoliation.

### 4.3 Water soluble carbohydrates

The concentration of water soluble carbohydrates (WSC) in stubbles of *F. pratensis* at defoliation was significantly higher than in *D. glomerata* (Fig. 4A). The WSC concentrations were with 6.4 % in *F. pratensis* and 3.2 % in *D. glomerata* rather low in both species. The WSC concentrations in *F. pratensis* dropped sharply after defoliation, reached a minimum after approximately one day and then increased to higher levels than before defoliation. In contrast, the WSC concentrations in *D. glomerata* were constant during the first three days of regrowth. In *F. pratensis* the WSC concentrations increased at a higher rate as compared to *D. glomerata* after three days of regrowth, leading to significantly higher WSC concentrations nine days after defoliation. Like the concentration, the WSC content in stubbles of *F. pratensis* was higher relative to *D. glomerata* at defoliation. After 21 days of regrowth, the content of stubble WSC of *F. pratensis* was lower as compared to *D. glomerata* (Fig. 4B) due to a lower WSC concentration and a lower stubble weight (Fig. 2B).
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Figure 4: Changes in concentration (A) and Ln-transformed content (B) of water soluble carbohydrates (WSC) in stubbles of *Festuca pratensis* (▼,●) and *Dactylis glomerata* (▼,□) during regrowth after defoliation. After defoliation, remaining leaf area was removed. Means of four replicates and standard errors (I) are shown.

4.4 Regrowth under low light intensity

Regrowth under low light intensity was used to separate the concurrent carbon supply from photosynthesis and from mobilised carbohydrate reserves. It also served to study the adaptive potential of the SLA of both species to changing light conditions during regrowth as they might occur in the field. Both grasses maintained a constant total plant dry weight over the experimental period of seven days (Fig. 5A). Therefore both species were just able to meet their carbon demands for respiration by photosynthesis at a light intensity of 20 μmol m⁻² s⁻¹. Leaf growth of *F. pratensis* under low light intensity was slower than in *D. glomerata* (Fig. 5B). As a consequence, *F. pratensis* produced a significantly lower total leaf area and a lower total leaf length (Fig. 5C) as compared to *D. glomerata* over the whole regrowth period. In contrast, the LWR of *F. pratensis* was, on average, significantly higher (Fig. 5D).
Figure 5: Ln-transformed total dry weight (A), leaf area per plant (B), leaf length per plant (C), and leaf weight ratio (D) of Festuca pratensis (▼,--) and Dactylis glomerata (●, —) during regrowth after defoliation at a light intensity of 20 μmol m⁻² s⁻¹. After defoliation, remaining leaf area was removed. Means and linear regressions are shown in (A). Means of four replicates and standard errors (I) are shown in (B, C &D).

The SLA response of *F. pratensis* during the first three days of regrowth at 20 μmol m⁻² s⁻¹ was similar to its response at 500 μmol m⁻² s⁻¹ (Fig. 6). After this period the SLA of *F. pratensis* grown at 20 μmol m⁻² s⁻¹ increased compared to plants grown at 500 μmol m⁻² s⁻¹, reaching a significantly higher SLA four days after defoliation. The SLA response of *D. glomerata* to the changed light intensity after defoliation was faster and stronger than the response of *F. pratensis*. If regrowth occurred at the low light intensity, the SLA of *D. glomerata* increased to higher values relative to reference plants already three
days after defoliation. With 716 cm² g⁻¹ compared to 450 cm² g⁻¹, *D. glomerata* reached a 59 % higher SLA than *F. pratensis* four days after defoliation.

![Graph showing the specific leaf area (SLA) of Festuca pratensis and Dactylis glomerata](image)

**Figure 6**: Response of the specific leaf area (SLA) of *Festuca pratensis* and *Dactylis glomerata* to regrowth after defoliation at a light intensity of 20 umol m⁻² s⁻¹ compared to the SLA response at 500 umol m⁻² s⁻¹. After defoliation, remaining leaf area was removed. Means of four replicates and standard errors (I) are shown.

### 4.5 Impact of stubble photosynthesis on regrowth after defoliation

Since all leaf area had been removed, photosynthesis of defoliated plants was restricted to the remaining leaf sheaths (stubble photosynthesis). The area of the remaining leaf sheaths of *F. pratensis* (10.3 cm²) was substantially lower than that of *D. glomerata* (18.7 cm²).

The restriction of stubble photosynthesis reduced the regrowth of both species (Fig. 7). However, the extent and duration of the reduction was much less pronounced in *F. pratensis* than in *D. glomerata*. Without stubble photosynthesis, Ln-transformed dry weights and RGR of *F. pratensis* were clearly but not significantly lower at all harvests during the first week of regrowth (Fig. 7A & B). In contrast, the loss of stubble photosynthesis considerably reduced the regrowth capacity of *D. glomerata* and significantly reduced the total plant dry
weight within two days after defoliation relative to reference plants (Fig. 7C). The reduced regrowth capacity of *D. glomerata* was associated with a negative RGR during the first two days after defoliation (Fig. 7 D).

**Figure 7**: Impact of stubble photosynthesis on regrowth after defoliation of *Festuca pratensis* (A & B) and *Dactylis glomerata* (C & D). Ln-transformed total dry weight and relative growth rate of both species are shown. After defoliation, remaining leaf area was removed. Second-order polynomials were fitted through the Ln-transformed dry weights in (A & C). Means of four replicates as well as fitted values are shown in (A & C). I represents the standard errors for the fitted values.

4.6 **The significance of stubble photosynthesis and stubble reserve carbohydrates for regrowth of *F. pratensis***

The WSC concentration in stubbles of *F. pratensis* grown at ambient CO₂ (approx. 450 ppm) was with 8.3 % slightly higher than in the previous
I Regrowth at non-limiting nutrient supply

experiments (Table 2). The CO₂ deprivation to 20 ppm for the last five days before defoliation significantly reduced the WSC percentage by 49 % and the WSC content by 78 %. Consequently in plants grown under CO₂ deprivation, the apparently available WSC reserves for regrowth were with only 1.5 mg per plant very low at defoliation.

Table 2: Impact of CO₂ deprivation for the last five days before defoliation on water soluble carbohydrates (WSC) in stubbles of Festuca pratensis. The WSC percentage and the WSC content of plants grown at ambient CO₂ (approx. 400 ppm) relative to plants grown under CO₂ deprivation (20 ppm) are shown. s.e. stands for standard errors of the means.

<table>
<thead>
<tr>
<th>CO₂ pre-treatment:</th>
<th>450 ppm</th>
<th>20 ppm</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>WSC %</td>
<td>8.3</td>
<td>4.2</td>
<td>0.11</td>
</tr>
<tr>
<td>WSC mg</td>
<td>6.8</td>
<td>1.5</td>
<td>0.30</td>
</tr>
</tbody>
</table>

Both the WSC pool at the time of defoliation and the stubble photosynthesis influenced the regrowth of F. pratensis after defoliation (Fig. 8). The significance of both factors was remarkably high immediately after defoliation and decreased during regrowth. After one week of regrowth, neither the reduction in the WSC pool nor in stubble photosynthesis had an impact on the RGR of F. pratensis. The CO₂ deprivation strongly reduced the total dry weight of the after defoliation remaining plant parts of F. pratensis relative to control plants grown at ambient CO₂ (Fig. 8A). The regrowth of F. pratensis after defoliation was not negatively affected by the 50 % reduction of stubble WSC concentration compared to control plants. In contrast, the RGR of F. pratensis with reduced stubble WSC was significantly higher during the first four days of regrowth compared to the control plants (Fig. 8B).

The stubble photosynthesis was of greater relevance for the regrowth of F. pratensis after defoliation than differences in the WSC pool of stubbles.
Independently of the WSC pool, the loss of stubble photosynthesis reduced RGR during the first four days of regrowth as compared to the control. However, the reduction in RGR was significant only for WSC depleted plants. Consequently, the loss of stubble photosynthesis was more aggravating for *F. pratensis* when WSC reserves were low.

Figure 8: The significance of stubble carbohydrate reserves and stubble photosynthesis for regrowth after defoliation of *Festuca pratensis*. Ln-transformed total dry weight (A), relative growth rate (B), Ln-transformed leaf area (C), and relative growth rate of leaf area (D) with and without stubble photosynthesis at two WSC levels are shown. After defoliation, remaining leaf area was removed. Second-order polynomials were used to fit the Ln-transformed total dry weights and leaf area in (A & C). Means of four to six replicates as well as fitted values are shown in (A & C). I represents the standard errors for the fitted values.
In contrast, leaf growth (Fig. 8C) and RGRLA (Fig. 8D) of *F. pratensis* was only slightly influenced by either of the treatments. Leaf growth and RGRLA of *F. pratensis* seemed, therefore, to be rather insensitive to the differences in WSC reserves or stubble photosynthesis tested in this experiment.

5. DISCUSSION

5.1 Lower regrowth capacity of *F. pratensis*

Regrowth after defoliation at non-limiting nutrient supply of both species was characterised by an initial period without dry weight gain, followed by a period of exponential growth. Regrowth capacity of *F. pratensis* was lower as compared to *D. glomerata*. Although both species had similar initial dry weights and tiller numbers, differences in the regrowth capacity resulted in a 18 % lower total dry weight of *F. pratensis* three weeks after defoliation. The slower regrowth capacity of *F. pratensis* was the result of a significantly lower mean RGR than *D. glomerata* (Table 1). The lower mean RGR in turn was mainly caused by a relatively slow regrowth of *F. pratensis* during the first two days after defoliation (Fig. 1A). During this initial period the total dry weight of *F. pratensis* remained at a constant level, while *D. glomerata* began to increase dry weight immediately after defoliation. Thus the lower dry weight accumulation of *F. pratensis* during the initial phase mainly determined the differences in weight at the end of the regrowth period.

In managed grasslands species with a high maximal RGR are competitively superior to slower growing species (Grime & Hunt 1975; Poorter 1989). In agreement with the present study the RGR of *F. pratensis* was lower than that of *D. glomerata*, independent of temperature and photoperiod in growth chamber experiments of Carlen (1994) and lower than the RGR of *Lolium multiflorum* in experiments of Bühring (1990). These results support the conclusion that an inherently slower regrowth capacity after defoliation might be an important factor limiting the shoot competitive ability of *F. pratensis* in permanent and sown grasslands at higher soil fertility.
The lower RGR of *F. pratensis* during the initial phase was the result of a slower increase in LAR (Fig. 1C), which was not compensated by a higher NAR (Fig. 1D). The increase in LAR of *F. pratensis* was limited by a generally lower SLA and a lower SLA response to defoliation (Fig. 1E). The slower replacement of leaf area during the first three days of regrowth (Fig. 3A), due to differences in SLA, was therefore mainly responsible for the lower regrowth capacity of *F. pratensis* relative to *D. glomerata*. The lower SLA was also the most important factor in the lower increase in total leaf area of *F. pratensis* during regrowth at low light intensity (Fig. 5B).

Producing more leaf area with the same resource investment can be a competitive advantage under light-limiting conditions (Holt 1995). A fast replacement of leaf area after defoliation is an important factor in competition for light (Grime 1979). In contrast to leaf area, the increase in average tiller length of *F. pratensis* after defoliation was higher relative to *D. glomerata* (Fig. 3D). The superior extension growth after defoliation might allow *F. pratensis* to shade *D. glomerata*. However, *F. pratensis* is known to have a low shoot competitive ability in the field (Carlen 1994). Therefore, the fast re-placement of leaf area after defoliation, independent of light intensity, might give *D. glomerata* more important advantages in competing for light in the field.

There were general morphological differences between the leaves of the two species. The SLA of *F. pratensis* was consistently lower over the whole regrowth period. In addition, *F. pratensis* required a longer time to increase its SLA in response to low light conditions during regrowth and its capacity of SLA increase was lower as compared to *D. glomerata* (Fig. 6). Regrowing plants in the field are subjected to fast changes in temperature and light conditions. Plants differ in their adaptability to reduced light conditions by redistribution of dry matter, altered leaf anatomy or decreased respiration and enzyme activity (Olff 1992; Holt 1995). A high capacity for fast morphogenetic adaptation to changes in environmental conditions is of great advantage in competing for both above- and below-ground resources (Grime 1979, Poorter 1989). A high SLA is an important determinant of a high RGR during regrowth and competitive ability (Poorter 1989; Poorter & Remkes 1990; Garnier 1992; Elberse & Berendse 1993).
F. pratensis is known for a low SLA relative to D. glomerata (Gügler 1993; Carlen 1994). Therefore, the generally lower SLA and the lower capacity to adapt its SLA to unfavourable growth conditions might be an additional important restriction for regrowth of F. pratensis in the field.

Despite increasing differences in total plant dry weight during the first two days of regrowth (Fig. 1A), LWR (Fig. 1F) and shoot yield (Fig. 2A) of both species increased at a similar rate. Consequently, F. pratensis allocated more resources to the re-establishment of photosynthetic surface than D. glomerata by curtailing root and stubble growth to a greater extent (Fig. 2B & C). This different allocation pattern after defoliation was manifested in a higher harvest index of F. pratensis (Fig. 2D) as well as in a delayed tillering after defoliation (Fig. 3C).

Due to its higher harvest index, a higher proportion of plant weight was removed by defoliation at all sequential harvests during the second half of the regrowth period. This led to reduced stubble and root dry weight at the next defoliation. A higher harvest index might have negative consequences for both the shoot and the root competitive ability of F. pratensis in a regularly defoliated sward. The lower stubble weight and tiller number would probably have reduced the regrowth rate of F. pratensis at subsequent harvests. The stronger curtailing of root growth and the lower root dry weight probably reduced its root competitive ability as compared to other grasses such as D. glomerata.

5.2 Significance of water soluble carbohydrates and stubble photosynthesis for regrowth

Besides of inherent differences in the capacity of each species, regrowth after defoliation of young vegetative forage grasses depends on the concurrent carbon supply from stored soluble carbohydrate reserves and from the photosynthesis of remaining plant parts. Regrowth is also affected by the allocation of these carbohydrates to shoot sinks and the efficiency of their utilisation (Richards 1993). In the present study all the remaining leaf area was removed. Therefore, defoliated plants depended on the photosynthesis of the remaining leaf sheaths and newly developed leaf area. The prevention of stubble photosynthesis only slightly affected the RGR of F. pratensis (Fig. 7B). In contrast, RGR of D. glomerata
was significantly reduced by the lost of stubble photosynthesis (Fig. 7D). The stubble area of *F. pratensis* (10.3 cm²) was substantially lower than that of *D. glomerata* (18.7 cm²). It is reasonable that the different RGR response of both species to the loss of stubble photosynthesis was related to these differences in green stubble area, even if no direct estimation of stubble photosynthesis was made.

Davies (1965) argued that in the field, water soluble carbohydrates in stubbles would affect regrowth, only if they fall below a critical level. This critical level would be approximately 16 to 20 % for field grown perennial ryegrass. Compared to these values, the WSC concentration and WSC content of both species at defoliation were very low in the present study (Fig. 4). Defoliation did not affect the WSC reserves in *D. glomerata* and reduced the WSC reserves in *F. pratensis* for just one day. Thus, a possible impact of WSC reserves on regrowth was restricted to a very limited period of time, because both species began to restore their WSC reserves already after the first day of regrowth. In *D. glomerata* the WSC concentration of 3.2% was probably already too low to be further depleted, as all assimilates were invested into plant growth rather than into WSC accumulation before defoliation. The lack of a WSC reduction during regrowth in *D. glomerata* might also indicate that the WSC depletion was too fast to be detected after one day or that all carbon necessary for regrowth was contributed by stubble photosynthesis. In *F. pratensis* there was no clear relationship between the WSC pool and regrowth after defoliation, because its RGR increased (Fig. 8B) after the WSC pool was reduced by 78 % (Table 2). Simultaneously, RGRLA increased as compared to references plants (Fig. 8D). Thus the depletion of WSC tended to cause an increased total photosynthate sink in *F. pratensis* which, in turn, probably increased the photosynthetic output of remaining plant parts (Davies 1974; Booysen & Nelson 1975). These results suggest that the impact of WSC reserves on regrowth of both species was negligible compared to the impact of the current stubble photosynthesis in the present study.

Both species maintained their initial dry weight during regrowth under low light conditions (Fig. 5). Consequently, both species were able to meet their carbon demands for respiration by photosynthesis at a light intensity of 20 μmol m⁻² s⁻¹.
Therefore, respiration losses of both species were either similar or differences were too small to be detected by this regrowth technique. The newly grown shoot material during regrowth at low light intensity consisted of leaves only. Similar to regrowth in full light, the increase in LWR (Fig. 5D) of *F. pratensis* was higher than that of *D. glomerata*. In contrast, *D. glomerata* produced a greater leaf area due to its faster and higher SLA response to defoliation (Fig. 6). Assuming similar respiration losses, the LWR increase in both species during regrowth at low light intensity reflects the ability of carbohydrate allocation to shoot sinks. It was not possible to determine whether these carbohydrates were provided by storage tissues or by current photosynthesis at 20 µmol m\(^{-2}\) s\(^{-1}\). However, it is concluded that the differences in the efficiency of carbon use for regrowth were small between the two species. Thus a lower stubble photosynthesis and differences in leaf attributes were probably the most important factors causing the lower RGR of *F. pratensis* relative to *D. glomerata* during the initial phase of regrowth in this study.

Soluble carbohydrate reserves are often considered to be the primary source of carbon for regrowth following defoliation of temperate grasses (Shread 1973; Deregibus, Tilica & Jameson 1982). However, in agreement with the present study, there is ample evidence that, in most cases, the current photosynthesis of the remaining leaf area is the most important carbon source for regrowth as long as regrowth is not limited by meristemmatic limitations (Booysen & Nelson 1975; Richards & Caldwell 1985; Danckwerts 1993; Richards 1993). In addition to these results, our study shows that differences in stubble photosynthesis can also have a significant effect on regrowth after defoliation. In the field, after defoliation remaining stubbles of *F. pratensis* were often covered by dead leaf sheaths, while leaf sheaths of *D. glomerata* were still green (Gügler 1993; Carlen 1994). Our findings support the hypothesis that regrowth of *F. pratensis* may be negatively influenced by a lower stubble photosynthesis after defoliation if all leaf area is removed by defoliation. This might be the case after growth cycles with reproductive tillers when most leaf area is carried above the level of defoliation due to stem elongation and reserves are low. In these situations, however, other factors such as differences in meristemmatic activity (Richards &
Regrowth at non-limiting nutrient supply

Caldwell 1985; Bassetti 1989) due to a relatively high proportion of reproductive tillers of *F. pratensis* (Gügler 1993; Carlen 1994), might represent more important restrictions for regrowth. In addition, the factors limiting regrowth of *F. pratensis* relative to *D. glomerata* might change during the growing season due, for example, to different responses of the two species to changes in temperature and photoperiod (Carlen 1994). Most times differences in remaining leaf area, the slower increase in LAR due to the lower SLA (Fig. 1), the higher harvest index (Fig. 2) and the longer period of delayed tillering (Fig. 3) might be more important restriction for regrowth of *F. pratensis* than differences in stubble photosynthesis.

### 5.3 Conclusions

*F. pratensis* had a lower regrowth capacity at non-limiting nutrient supply than *D. glomerata*, caused mainly by a period in which dry weight did not increase during the first two days of regrowth. This period was the result of slower leaf area development after defoliation. The slower leaf growth of *F. pratensis* was, to a great extent, related to a lower stubble area and a lower SLA response to defoliation. Differences in WSC reserves, in the efficiency to allocate stored WSC reserves to shoot sinks, and carbon losses by respiration were less important.

Therefore, the shoot competitive ability of *F. pratensis* in grasslands might be limited by an inherently lower regrowth capacity after defoliation at high soil fertility due to a slower replacement of leaf area during the initial phase of regrowth. The low shoot competitive ability of *F. pratensis* might also be related to its generally lower SLA, a lower potential for morphogenetic adaptation to changes in the environment or to other factors. Regrowth of *F. pratensis* and its impact on shoot competitive ability has to be further investigated.
PART II

SEASONAL VARIATION OF PLANT ARCHITECTURE AND ITS CONSEQUENCES FOR THE SHOOT COMPETITIVE ABILITY OF FESTUCA PRATENSIS AND DACTYLIS GLOMERATA

1 SUMMARY

Differences in the seasonal variation of plant architecture can have important implications for the competitive ability of grasses. Our objective was to analyse the effects of season and shoot competition on above- and below-ground plant traits and to assess the consequences for shoot competitive ability in a regularly defoliated grassland. Festuca pratensis Huds. (Meadow fescue), a weak shoot competitor, and Dactylis glomerata (Orchard grass), a strong shoot competitor, were grown in intraspecific and interspecific shoot competition in the field for two years. With fully destructive harvests, the effects of season and shoot competition on canopy structure, biomass allocation in the whole plant, and the content of water soluble carbohydrates (WSC) were assessed. The effects of season and shoot competition on root activity in different soil layers were estimated from the uptake of the non-radioactive tracers, rubidium and lithium. 

D. glomerata, the stronger shoot competitor, allocated more biomass to the stubbles, and had, on average, a higher total WSC content as well as a generally higher root activity. F. pratensis, the weaker competitor, was characterised by a generally higher biomass allocation to the roots and a low root activity. The shoot competitive ability of F. pratensis changed strongly with season. Despite a relatively high competitive ability during reproductive growth and in autumn, the shoot competitive ability of F. pratensis decreased due to the negative effects of a lower shoot competitive ability during vegetative growth in summer. The decreasing shoot competitive ability of F. pratensis during summer was the result of shading caused by a lower leaf area proportion in the upper canopy layers.

F. pratensis responded to shading with reduced tillering, lower WSC accumulation in stubbles and roots, and a higher biomass allocation to harvested
plant parts, while *D. glomerata* showed the opposite response. Due to the species specific response of biomass allocation to above- and below-ground plant parts, interspecific shoot competition mainly affected root and stubble weight and, to a lesser extent, the harvestable shoot yield.

It is concluded that the high competitive ability of *D. glomerata* may be related to its ability to exploit above- and below-ground resources after defoliation faster than *F. pratensis* but that the parameters limiting the shoot competitive ability of a species probably change with season.

2 INTRODUCTION

Plant competition is a process that occurs through the negative effects that individual plants have on resource availability to neighbouring individuals (Tremmel & Bazzaz 1993). Plants mainly compete for light and for mineral nutrients and water (Donald 1963). In order to obtain undepleted resources before they are consumed by other species, the spatial arrangement of leaf layers (Berendse & Elberse 1989; Barnes et al. 1990; Holt 1995) and of roots (Berendse 1982; Caldwell & Richards 1986; Fitter 1992) as well as the nutrient acquisition rate of roots (Grime 1977; Lambers & Poorter 1992; Ryser & Lambers 1995) may be important determinants of competitive ability. Because of the rapid extinction of visible radiation in canopies (Saeki 1963), the ability of a plant to place foliage in the upper, well-lit canopy layers is an important structural trait contributing to shoot competitive ability (Caldwell 1987; Barnes et al. 1990; Holt 1995). In addition, the shoot competitive ability of a species and the parameters affecting shoot competition will probably change with season, due, for example, to differences in the species-specific response of plant architecture to the seasonal changes in environmental conditions. However, only a small number of field experiments on shoot competition with regularly defoliated pasture plants were long enough to study the seasonal change in shoot competition (Remison & Snaydon 1980; Carlen 1994). In addition, these studies focused on the response of above-ground attributes to shoot competition only. The whole plant response would be more appropriate, because plants face an unavoidable trade-off in
Seasonal variation of shoot competition

competing for limited resources due to the physical separation of above- and below-ground resources (Tillman 1988). If, for example, one species has to allocate more biomass to the shoot in response to shoot competition, then this might well be at the expense of root and stubble weight or the accumulation of reserves which, in turn, might reduce the plant's ability to compete for limited resources at a later stage.

In cooler regions, Festuca pratensis Huds. (Meadow fescue) is an excellent herbage grass with good forage quality, winterhardiness and adaptation to humid conditions. It is however a weak competitor in fertile soils, barely affected by management intensity (Mott 1982; Meister & Lehmann 1990; Gügler 1993). Carlen (1994) analysed the seasonal effects of shoot and root competition on F. pratensis and Dactylis glomerata (Orchard grass). The study showed that the competitive ability of F. pratensis was mainly limited by a low shoot competitive ability. Shading, due to differences in the seasonal change in canopy structure as compared to companion grasses, might be one important factor contributing to the low shoot competitive ability of F. pratensis. Further knowledge is needed about the plant traits which determine the outcome of competition in a regularly defoliated sward and about the processes limiting shoot competitive ability of a species under the rapid seasonal changes of environmental conditions.

In this study, we investigated the effects of season and shoot competition on above- and below-ground plant traits of F. pratensis and D. glomerata under field conditions. Our aims were: (1) to assess the seasonal change in canopy structure of the two grasses and evaluate its consequences for shoot competitive ability; (2) to assess the effects of season and canopy structure on biomass allocation of the two species to above- and below-ground plant parts; and (3) to assess the effects of interspecific shoot competition on biomass allocation, reserve accumulation, stubble growth, root growth, and root activity in different soil layers.

It will be demonstrated convincingly that shoot competition is a dynamic process affecting above- and below-ground plant parts and changes with nearly every regrowth, depending on slight differences in the species response to the changes in environment.
3 MATERIALS AND METHODS

3.1 Experimental method

A field experiment on shoot competition was carried out from October 1993 to October 1995 at the research station of the Swiss Federal Institute of Technology in Eschikon, near Zurich, Switzerland (550 m above sea level). The experiment was a completely randomised block with four replications (four forcing beds of 10 x 1.45 m) with two forms of shoot competition. Each forcing bed consisted of two swards (2.56 x 1.38 m) with either Festuca pratensis (Meadow fescue) or Dactylis glomerata (Orchard grass) in intraspecific shoot competition and a sward (4.24 x 1.38 m) with the two species in interspecific shoot competition. Root competition was separated using the experimental technique based on Donald (1963), adapted for full destructive sequential harvesting. The soil of the forcing beds was removed and polystyrol partitions, held together by thread posts, were inserted. In intraspecific shoot competition, the partitions divided the soil of the plots into 36 compartments, 1.2 x 0.06 x 0.45 m, and in interspecific shoot competition into 64 compartments. The compartments were caulked of each other to prevent the intermingling of roots. Two boxes (0.60 x 0.40 x 0.45 m) were installed at the front of each plot and were used as movable borders. After inserting the polystyrol partitions and the movable borders, the forcing beds were carefully refilled with a 80/20 volume percent mixture of strained fertile soil and sand (0 - 3 mm) to a height of 0.45 m.

3.2 Experimental set-up, establishment, and growth conditions

Seedlings of F. pratensis Huds. cv. Predix (RAC, CH) and D. glomerata L. cv. Baraula (Barenbrug, NL) were grown in quick-pots in the glasshouse for 35 days. Selected plants were transplanted into the forcing beds outdoors from 1 to 6 October 1993. In intraspecific shoot competition, plants of one species were planted row-wise into the compartments at a density of 278 plants m\(^{-2}\) (planting distance 0.06 x 0.06 m). In interspecific shoot competition, the two species were
planted in alternate rows in a 0.5:0.5 replacement design (Fig. 9). Each row consisted of 23 plants, the innermost eight of which were used for analysis. The rest of the plants served as a border, 0.48 m (south side) and 0.42 m (north side) along the lateral sides of the plots. There was also a border of 0.40 m along the front side of each plot.

In March 1994 and 1995, all treatments were supplied with 5 g P/m², 26 g K$_2$O/m², and 3 g Mg/m² dissolved in water. Nitrogen was applied in spring before growth started and one day after each defoliation, in a solution of NH$_4$NO$_3$ at a rate of 32 g N m$^{-2}$ year$^{-1}$. The plots were irrigated during summer so that water did not limit growth. Unwanted plant species were removed throughout the experiment.

**Figure 9**: Experimental set-up showing *Festuca pratensis* (F) and *Dactylis glomerata* (D) in intraspecific shoot competition and in interspecific shoot competition. Plants were grown row-wise in compartments of 1.2 x 0.06 x 0.45 m held together by thread posts to prevent root competition between plant rows. In intraspecific shoot competition, plants of one species were planted row-wise into the compartments at a density of 278 plants m$^{-2}$ (FF, DD). In interspecific shoot competition, the two species were grown in alternate rows in a 0.5:0.5 replacement design (FDFD).
3.3 Harvesting procedure

The swards were defoliated six times per growing season: in 1994 on 20 May, 21 June, 21 July, 18 August, 15 September, and 18 October and in 1995 on 17 May, 21 June, 20 July, 22 August, 18 September, and 19 October.

At each harvest during intraspecific and interspecific shoot competition one plant row and two plant rows respectively were removed from the swards and harvested fully destructively. A new sampling technique was developed for sequential harvesting and stratified clipping. The technique allowed precise and efficient harvesting and stratified clipping of the whole plants, independent of season and weather. Undisturbed plant rows were made accessible by removing the boxes with the border plants at the front of the swards and the lateral polystyrol partition of the root compartment (Fig. 10A, B). A specially designed plate was pressed vertically against the root compartment of the selected plant row. The root compartment of the plant row was loosened and the plant row placed on the plate. The plate was slowly turned from a vertical to a horizontal position and the plant row removed from the sward.

The shoots of the plant row were gently pressed. The press (0.96 x 0.6 m) consisted of a central element (0.48 x 0.6 m) and two lateral elements (0.24 x 0.6 m) all of which could be taken apart. The central element could again be separated (starting at the top: two elements 0.48 x 0.15 m, one element 0.48 x 0.12 m, one element 0.48 x 0.08 m, and two elements 0.48 x 0.05 m). After removing the lateral elements of the press, the shoot and stubble fractions of the border plants were cut away and eliminated. The shoots of the eight innermost plants (0.48 x 0.6 m) remained under the central part of the press. A template was used to determine the corresponding root volume of the sample plants, and the root volume of the border plants was removed. The remaining plants under the press were used for stratified clipping and further investigations. Using the template, the root compartment of the sample was divided into three layers at depths of 0-0.12 m, 0.12-0.24 m, and 0.24-0.36 m and removed. Plants were defoliated 0.05 m above the root system to give the stubble fraction. Stratified clipping of the shoots took place, starting at the top of the sample plants, by
removing element per element of the press. Depending on the season, biomass in three to seven canopy layers (0.80-0.65, 0.65-0.50, 0.50-0.35, 0.35-0.23, 0.23-0.15, 0.15-0.10, 0.10-0.05 m above the surface of the soil) was harvested. After the sequential harvests, thread posts were cut back to the next compartment secured by screws, the boxes with the border plants reinstalled and the rest of the swards defoliated to 0.05 m above the soil surface.

Figure 10: (A) A plant row of *D. glomerata* in intraspecific shoot competition, ready to be harvested fully destructively, after removal of the border plants and the lateral polystyrol partition of the plant row. (B) „Press“ (0.96 x 0.6 m) composed of different elements used for stratified clipping of the sample plants.
3.4 Plant measurements

The biomass of each canopy layer was separated into leaf lamina and leaf sheaths (Fig. 11). Leaf area was measured with a photoelectric meter (Model Li-3000 A; Li-Cor Inc. Lincoln, NE, USA). Stubbles were washed, senescent tillers removed, and the tiller number determined. A tiller counted, if it was longer than 0.05 m. A subsample of 40% of the stubble fraction was separated into senescent leaf sheaths and green plant material for later determination of the content of water soluble carbohydrates and the total stubble dry weight. Roots were washed out by rinsing the soil samples on a sieve with a mesh gauge of 1.25 mm. All samples were dried at 65°C for 48 hours and the dry weight determined.

Figure 11: Fractionation and measurements to determine the effects of season and shoot competition on above- and below-ground plant traits of *F. pratensis* and *D. glomerata* in intraspecific and interspecific shoot competition. Plants were grown under field conditions and defoliated six times per growing season in 1994 and 1995. Sequential harvests were made at the end of each regrowth period.
3.5 Measurement of light transmission

The vertical distribution of the photosynthetic active photon flux density (PPFD) in the canopies was measured at the harvests on 21 June, 21 July, 18 August, 15 September, and 18 October in 1994 and 15 May, 21 June, 20 July, and 22 August in 1995. PPFD was determined by means of a Decagon Sunfleck Ceptometer (Decagon Devices Inc., USA) with a light sensitive area of 800 x 10 mm placed horizontally into the canopy 0.12, 0.19, 0.29 m (in 1995 only) and 0.42 m (during reproductive growth only) above-ground. The relative PPFD was calculated against a reference PPFD above the canopy to give the seasonal pattern of light transmission (T) in the canopy.

3.6 Response to shoot competition

Resource complementarity (Snaydon & Satorre 1989), i.e. the extent to which two species share common limiting resources, was determined according to the relative yield total (RYT) (de Wit 1960). RYT, based on the total dry weight, did not differ significantly from 1.0. Thus, the two species showed no resource complementarity, indicating that they fully competed for the same limiting resources.

The shoot competitive ability was determined with the competitive balance index (Wilson 1988), based on the total dry weight per plant. At a RYT of 1.0, variation in the competitive balance index depends on competition effects and can be interpreted as competitive ability. The competitive balance index (Cbij) of *F. pratensis* (species i), relative to *D. glomerata* (species j), for a 0.5:0.5 replacement design is:

\[
Cbij = \log_e\left(\frac{W_{ij}}{W_{ji}}\right) / \left(\frac{W_{ii}}{W_{jj}}\right)
\]

Wij and Wji is the total dry weight per plant of *F. pratensis* and *D. glomerata* respectively, grown in interspecific shoot competition. Wii and Wjj is their total dry weight when grown in intraspecific shoot competition.
A C\text{bij} of zero indicates that both species have the same shoot competitive ability. A positive C\text{bij} indicates that \textit{F. pratensis} has a higher shoot competitive ability than \textit{D. glomerata}. A negative C\text{bij} indicates that \textit{F. pratensis} was less competitive than \textit{D. glomerata}. C\text{bij}, as a measure of shoot competitive ability, has the advantage that the values are not limited as compared to, for example, aggressivity (values between 1 and -1) (Mcgilchrist & Trenbath 1971).

3.7 Water-soluble carbohydrate analyses

Approximately 10 mg of finely ground plant material were extracted in 1 cm$^3$ of 80% (v/v) ethanol in water at 80 °C for 30 min. After centrifugation at 15000 x g for 15 min, the supernatant was retained and the pellet re-extracted with 1 cm$^3$ of water in a sonicator at approximately 45 °C for 15 min. After centrifugation as above, the combined supernatants were used for carbohydrate extraction with the anthrone method (Dreywood 1946). The anthrone reagent was similar to that described by Deriaz (1961): 350 cm$^3$ of water, 735 cm$^3$ concentrated H$_2$SO$_4$ ($p=1840$ kg m$^{-3}$), 10 g of thiourea and 865 mg of anthrone. Five cm$^3$ of ice-cold anthrone reagent was added and the reaction mixture vigorously mixed. The tubes were arranged in racks of 60, covered with marbles and incubated in a water bath at 96.2 °C for 40 min. After 30 min at room temperature each sample was mixed, and the absorption at 625 nm was measured. All reactions were performed in duplicate.

3.8 Root activity

Rubidium (Rb) and lithium (Li) served as non-radioactive tracers to determine the root activity at soil depths of 0.06 and 0.30 m. Rb and Li are taken up in a similar manner as potassium. They are non-toxic in concentrations that are already determinable, are not easily leached, and are of low natural concentrations in the soil (Fitter 1986). In this experiment, the natural concentrations varied between 6 and 24 ppm Rb and between 2 and 16 ppm Li for both grasses. Root activity was measured as Rb and Li uptake per shoot. The
14 innermost plants per root compartment were marked with Rb and Li tracer solutions. The tracer solutions were injected into the soil at 13 application points per root compartment, midway between two plants. A syringe which refilled automatically (Socorex ISBA S.A., CH) was used to inject 4 ml tracer solution per application point at soil depths of 0.06 m (40 mg Rb as RbCl diluted in water) and at 0.30 m (40 mg Li as LiCl diluted in water). In spring (20 April 1994 and 21 April 1995) and on the first day of regrowth after the last defoliation, the compartments for the next sequential harvest, 26 to 34 days later, were marked. A random sample of 8 to 10 tillers of the four innermost plants, defoliated at ground level, was used for the analyses. After senescent tissues were removed, the plant material was dried at 65 °C for 48 h.

All analyses were performed in the laboratory of Prof. Frossard at the Institute of Plant Sciences in Lindau-Eschikon, Switzerland. A subsample of approximately 250 mg was ashed at 540 °C for six hours. The ashes were dissolved in 2 ml HCl (20 % v/v) for 15 minutes at 70 °C and transferred to 50 ml flasks to which 1 ml of CsCl solution (80 g CsCl/l) was added. The volume was adjusted to 50 ml with distilled water and filtered (meshwidth 0.8 μm). The Rb content of the filtrate was determined by an atomic absorption spectrophotometer (Perkin-Elmer 5000) and Li by emission (ICP, Model Varian Liberty 200).

3.9 Statistical analysis

All statistical analyses were calculated with the SAS statistical package (Statistical Analyses System, Version 6.10, SAS Institute Inc., Cary, North Carolina, USA). Analyses of variance and standard error of the means (s.e.) were calculated according to the GLM procedure. Data were Ln-transformed before analyses of variance if variances were not distributed normally and not homogeneous. At the harvests on 18 August, 15 September, and 18 October 1994, two replicates of F. pratensis, grown in intraspecific shoot competition, were excluded from analyses, because the plants were infected by root aphids (Geoica setulosa, Pass., 1860).
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4 RESULTS

4.1 Seasonal variation in total plant dry weight and shoot competitive ability.

The total dry weight per plant of *F. pratensis* in intraspecific shoot competition was generally lower than that of *D. glomerata* in 1994 (Fig. 12A). Differences in total dry weight per plant increased strongly from the first to the second defoliation but decreased again at subsequent harvests. At the first two harvests in 1995, however, total plant weight per plant of *F. pratensis* was equal to and thereafter always exceeded that of *D. glomerata*.

In interspecific shoot competition, *F. pratensis* produced less total dry weight per plant than in intraspecific shoot competition, while *D. glomerata* increased its dry weight (Fig. 12B). These different responses to interspecific shoot competition led to an overall decrease in shoot competitive ability, measured as the competitive balance index of *F. pratensis* relative to *D. glomerata* during the two years (Fig. 12C). The overall effects of shoot competition, expressed as the mean competitive balance index decline per year, were slightly but not significantly higher in 1994 (-0.253) than in 1995 (-0.185). The shoot competitive ability of *F. pratensis* changed with season in both years. In 1994, the shoot competitive ability of *F. pratensis* was highest in May and decreased during summer, but increased again from September to October. In 1995, the shoot competitive ability of *F. pratensis* was relatively high until June, decreased from June to July, and then slowly increased again from July to October.
Figure 12: Seasonal change in total dry weight per plant in intraspecific shoot competition (A), relative total dry weight in interspecific shoot competition (B), and competitive balance index (C) in interspecific shoot competition (C) of Festuca pratensis (■, ▼) relative to Dactylis glomerata, (□, ○) over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
4.2 Seasonal effects of shoot competition on shoot, stubble, and root dry weight

In 1994 *F. pratensis* produced a higher shoot yield per plant in intraspecific shoot competition during the first growth cycle and in autumn but yields were considerably lower than those of *D. glomerata* at the second and third defoliations (Fig. 13A). In 1995, however, the course of harvested shoot dry weight of the two species was similar. The stubble dry weight of *F. pratensis* was, on average, 30% lower in 1994 but comparable to the stubble weight to *D. glomerata* after June 1995 (Fig. 13B). In contrast to the stubble fraction, the root dry weight of *F. pratensis* was always higher than that of *D. glomerata* after July 1994 (Fig. 13C).

There was strong seasonal variation in the effects of interspecific shoot competition on the dry matter distribution of the two species in both years (Fig. 14). Interspecific shoot competition strongly affected the dry weight of stubbles and roots of both species, while the effects on shoot dry weight were weak. Compared to the dry weights in intraspecific shoot competition, the effects increased from spring to mid August, leading to increasingly suppressed stubble and root growth of *F. pratensis* and enhanced growth of *D. glomerata*, and then decreased again until the end of the season (Figs 14B & C). Averaged over the two harvests in July and August 1995, the differences in the response of the two species to interspecific shoot competition resulted in a relative stubble dry weight of 0.75 for *F. pratensis* as compared to 1.43 for *D. glomerata* (Fig. 14B). Averaged over the same period, the relative root dry weight was 0.61 for *F. pratensis* and 1.51 for *D. glomerata* (Fig. 14C).
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Figure 13: Seasonal change in shoot dry weight (A), stubble dry weight (B), and root dry weight (C) of Festuca pratensis (■) and Dactylis glomerata (□) in intraspecific shoot competition over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (±) are shown.
Figure 14: Seasonal change in relative shoot dry weight (A), relative stubble dry weight (B), and relative root dry weight (C) of Festuca pratensis (▼) and Dactylis glomerata (○) in interspecific shoot competition over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
4.3 Seasonal effects of shoot competition on biomass allocation to shoots and roots

The biomass allocation to the stubbles and roots of the two species in intraspecific shoot competition was generally different (Figs 15B & C). The stubble weight ratio of *F. pratensis* (on average 0.34) was considerably lower as compared to *D. glomerata* (0.46) (Fig. 15B). In agreement with the higher root dry weights, the root weight ratio of *F. pratensis* was generally higher (on average 0.38) than that of *D. glomerata* (0.28) (Fig. 15C).

The differences in biomass allocation to the shoots of the two species changed with season (Fig. 15A). The shoot weight ratio of *F. pratensis* was significantly higher (0.58) than that of *D. glomerata* (0.51) at the first defoliation on 20 May 1994. In contrast, the shoot weight ratio of *F. pratensis* was considerably lower than that of *D. glomerata* from June to August but significantly higher in September and October in both years. Thus, the biomass investment of *F. pratensis* to harvested shoot parts was higher as compared to *D. glomerata* during periods of relatively high shoot competitive ability in spring and autumn. During periods of decreasing shoot competitive ability in summer, however, in intraspecific shoot competition *F. pratensis* allocated the largest part of its assimilates to the roots but considerably less biomass to the harvested shoot parts and the stubbles. In contrast, *D. glomerata* allocated most of its assimilates to the stubbles and the harvested shoot parts during this period.
Figure 15: Seasonal change in shoot weight ratio (A), stubble weight ratio (B), and root weight ratio (C) of *Festuca pratensis* (■) and *Dactylis glomerata* (□) in intraspecific shoot competition over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
The different seasonal effects of interspecific shoot competition on above- and below-ground plant parts (Fig. 14) were caused mainly by a change in the seasonal pattern of biomass allocation of both species relative to intraspecific shoot competition (Figs 16 & 17).

**Figure 16:** Seasonal change in shoot weight ratio (A), stubble weight ratio (B), and root weight ratio (C) of *Festuca pratensis* in intraspecific shoot competition (■) and in interspecific shoot competition (□) over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
Figure 17: Seasonal change in shoot weight ratio (A), stubble weight ratio (B), and root weight ratio (C) of *Dactylis glomerata* in intraspecific shoot competition (□) and in interspecific shoot competition (□) over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
During the reproductive growth cycle in 1994 and during periods of decreasing shoot competitive ability during summer in both years, *F. pratensis* significantly increased its shoot weight ratio in interspecific shoot competition (Fig. 16A). Compared to intraspecific shoot competition, this response resulted in a 21 to 26% higher shoot weight ratio in interspecific shoot competition from July to August in both years. In summer 1994, the higher biomass allocation to harvested plant parts led to a 6 to 9% lower stubble weight ratio and a 4 to 7% lower root weight ratio (Figs 16B & C). In summer 1995, the higher shoot weight ratio in interspecific shoot competition was compensated by a significantly lower root weight ratio (18 to 19%).

*D. glomerata* responded to the different competitive situation in the mixtures with a reduced shoot weight ratio from July to August in both years hence in contrast to *F. pratensis* (Fig. 17A). On the other hand, interspecific shoot competition had no significant effects on the seasonal change in stubble weight ratio (Fig. 17B) and root weight ratio (Fig. 17C) of *D. glomerata*. 
4.4 Seasonal effects of shoot competition on canopy structure

The distribution of leaf area density in the three to seven horizontal compartments was used to characterise the seasonal change in canopy structure of *F. pratensis* and *D. glomerata* in intraspecific shoot competition in 1994 and 1995 (Fig. 18). The seasonal change in canopy structure of the two species in intraspecific shoot competition differed greatly. The species-specific differences in canopy structure changed with developmental stage and season and appreciably influenced the relative leaf area distribution in interspecific shoot competition. Both species were in the reproductive stage at the first defoliation in May 1994 and 1995 and in the vegetative stage at subsequent defoliations.

At the defoliation in May 1994, both species reached a canopy height of 0.65 to 0.80 m in intraspecific shoot competition. The leaf area density of *F. pratensis* was similar to that of *D. glomerata* in the strata between 0.50 and 0.80 m but was lower in the lower canopy layers. In interspecific shoot competition, *F. pratensis* reached a higher relative leaf area density than *D. glomerata* in the uppermost canopy layer, but, as in intraspecific shoot competition, had lower leaf area densities in the lower canopy strata.

During the period from June to the middle of August, the two species showed different patterns of vertical leaf area distribution in intraspecific shoot competition. Except at the harvest in June, *F. pratensis* and *D. glomerata* extended comparable leaf area densities in the strata between 0.05 and 0.15 m. However, *F. pratensis* reached a plant height of only 0.23 to 0.35 m, while *D. glomerata* grew to 0.35 to 0.50 m. As a result, the leaf area density of *F. pratensis* was considerably lower than that of *D. glomerata* in the strata above 0.15 m. In *F. pratensis* swards, the transmission of PPFD through the canopy was always higher than in *D. glomerata* swards. From June to the middle of August light transmission at 0.19 m above the soil surface was, on average, 94 % in *F. pratensis* swards as compared to 38 % in *D. glomerata* swards and at 0.12 m it was still 48 % in *F. pratensis* swards relative to 14 % in *D. glomerata* swards. In interspecific shoot competition, *F. pratensis* plants had either no leaves in the
uppermost canopy layers or only a very low leaf area density relative to *D. glomerata*. Light transmission through the canopy in interspecific shoot competition was intermediate to the contrasting light transmission of the two species in intraspecific shoot competition.

At the harvest in October, both species again reached approximately similar canopy heights and canopy structures, independent of the competition treatment. In contrast to 1994, the species-specific differences in canopy structure were marginal at the first defoliation in 1995 and were not affected by the competition treatment. However, despite similar leaf area and leaf area distribution in swards with intraspecific shoot competition, the transmission of PPFD in the upper canopy layers was higher in *F. pratensis* swards than in *D. glomerata* swards.

From June to the middle of August, *F. pratensis* again reached a height of only 0.23 to 0.35 m in swards with intraspecific shoot competition, while the uppermost leaves of *D. glomerata* were found in the canopy layer from 0.35 to 0.50 m. In contrast to 1994, the leaf area density of *F. pratensis* in the strata between 0.05 and 0.15 m was usually higher relative to *D. glomerata*. The total light interception of *F. pratensis* from June to August, measured 0.12 m above the soil surface, was, on average, higher (81%) than in 1994 but still lower than for *D. glomerata* (91%).

In interspecific shoot competition, the leaves of *F. pratensis* were again found in the lower strata of the canopy only. Assuming a similar leaf inclination of both species, an estimate of light interception, based on relative leaf area density and light extinction in the different canopy layers above 0.1 m from June to August, shows that only 36% of the PAR was intercepted by *F. pratensis* and the rest by *D. glomerata*.

From September to October, both species again reached approximately the same canopy height, independent of the competition treatment.

Figure 18: Seasonal change in vertical distribution of *Festuca pratensis* (○) and *Dactylis glomerata* (□) leaf area density in intraspecific shoot competition and relative leaf area density in interspecific shoot competition over two growing seasons. The curves represent the transmission of photosynthetic photon flux density. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
4.5 Seasonal effects of shoot competition on tiller number

Except at the second regrowth in 1994, the number of tillers per plant of *F. pratensis* in intraspecific shoot competition was always higher as compared to *D. glomerata* (Fig. 19A).

![Graph](image_url)

**Figure 19:** Seasonal change in tiller number per plant of *Festuca pratensis* (■, ▼) and *Dactylis glomerata* (□, ◦) in intraspecific shoot competition (■, □) and in interspecific shoot competition (▼, ◦) over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.

Differences in tiller number increased drastically in 1995. After the reproductive growth cycle in spring, *F. pratensis* again reached a maximum of 26.6 tillers per plant at the harvest on 21 July. In contrast to *F. pratensis*, the tiller number of
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*D. glomerata* decreased strongly to a minimum of 9.4 tillers per plant from spring until the July harvest and then increased again. Interspecific shoot competition generally reduced the tiller number per plant of *F. pratensis* in both years, while *D. glomerata* increased its tiller number relative to intraspecific shoot competition (Fig. 19B). The effects of interspecific shoot competition increased from spring until the middle of the summer and then decreased again during the autumn of both years.

### 4.6 Seasonal effects of shoot competition on the content of water soluble carbohydrates per tiller

The seasonal change in the total content of water soluble carbohydrates (WSC) per tiller gives an indication about the source-sink relations in the plants. High WSC contents per tiller suggest that the carbon supply of source tissues surpasses the demand of growing tissues. Figure 20 shows the effect of season and shoot competition on the total WSC content per tiller of the stubbles and the root fraction at a soil depth of 0 to 0.12 m.

In 1994, the WSC content per tiller of *F. pratensis* in intraspecific shoot competition (on average 12 mg) was highly significantly lower at all harvests, except in June (Fig. 20A), than the WSC content per tiller of *D. glomerata* (24 mg). With only 5 mg per tiller at the first defoliation and 3 mg at the second defoliation, the WSC content of *F. pratensis* reached very low levels and recovered thereafter slower than in *D. glomerata*. In 1995, the WSC content per tiller of *F. pratensis* (10 mg) and *D. glomerata* (14 mg) was, on average, lower than in 1994, and the species-specific differences were far not as pronounced.

Both species responded to interspecific shoot competition with a reduced WSC content per tiller at the first defoliation in spring in both years as compared to intraspecific shoot competition, but responded differently from June to September (Fig. 20B). While the relative WSC contents of *D. glomerata* recovered to the values found in intraspecific shoot competition during the second regrowth and were not influenced until the end of season, interspecific shoot competition caused a reduction in the relative WSC contents of *F. pratensis*. The reduction of
the WSC content per tiller of *F. pratensis* in interspecific shoot competition increased to 25 % from May to June in 1994 and up to 65 % from May to July in 1995 and thereafter decreased again until September in both years.

**Figure 20**: Seasonal change in total water soluble carbohydrate (WSC) of the stubble and root fractions (0-0.12 m soil depth) per tiller of *Festuca pratensis* (■, ▼) and *Dactylis glomerata* (□, ○) in intraspecific shoot competition (■, □) (A) and in relative WSC content in interspecific shoot competition (▼, ○) (B) over two growing seasons. Plants were defoliated six times per growing season. Mean values and standard errors (I) are shown.
4.7 Seasonal effects of shoot competition on root activity in different soil layers

The uptake of the non-radioactive tracers rubidium (Rb) and lithium (Li) is indicative for the seasonal pattern of resource acquisition in different soil layers. The root dry weight per tiller at depths of 0 to 0.12 m and the Rb uptake at 0.06 m were used to determine the average specific absorption rate (SAR) from 0 to 0.12 m (Fig. 21). The SAR at depths between 0.24 and 0.36 m was determined together with the respective root dry weights per tiller at 0.24 to 0.36 m and with the Li uptake at 0.30 m soil depth (Fig. 22).

4.7.1 Root activity at 0 to 0.12 m soil depth

The average uptake of rubidium per month at a soil depth of 0.06 m in intraspecific shoot competition of F. pratensis relative to D. glomerata was 59% lower in 1994 and as much as 69% lower in 1995 (Fig. 21A). In 1994, the Rb uptake per tiller of both grasses was highest during reproductive development in May and decreased in June. In 1995, the Rb uptake during the first growth cycle was lower but remained at the same level during the second regrowth. From June to October the Rb uptake of F. pratensis in intraspecific shoot competition remained at a low level. In contrast, the Rb uptake of D. glomerata again reached a maximum in July 1994 and August 1995.

The specific absorption rate at soil depths of 0 to 0.12 m of F. pratensis swards was, on average, 43% lower than that of D. glomerata swards in 1994 and 63% lower in 1995. (Fig. 21C). Because the species differences in root dry weight per tiller were relatively low (Fig. 21B), the differences in SAR probably played a more important role in the differences in total Rb uptake.

Interspecific shoot competition did not affect the SAR of the two species in 1994. In 1995, the Rb uptake of F. pratensis in interspecific shoot competition was positively influenced by a higher SAR as compared to intraspecific shoot competition from June to July.
Figure 21: Seasonal change in rubidium uptake per tiller from 0.06 m soil depth (A), root dry weight per tiller in 0 to 0.12 m soil depth (B), and specific absorption rate for Rb in 0 - 0.12 m soil depth (C) of Festuca pratensis (▼, ▲) and Dactylis glomerata (●, ○) in intraspecific (▼, ●), and interspecific (▲, ○) shoot competition over two growing seasons. Mean values and standard errors (I) are shown.
4.7.2 Root activity at 0.24 to 0.36 m soil depth

Compared to the Rb uptake, the lithium uptake of *F. pratensis* at a soil depth of 0.30 m was approximately 12 to 14 times lower and that of *D. glomerata* 5 to 10 times lower (calculated from Figs 21 & 22). The seasonal course of Li uptake of the two species followed that of the Rb uptake. Independent of shoot competition, the monthly Li uptake per tiller of *F. pratensis* was much lower than that of *D. glomerata* in both years (Fig. 22A). In intraspecific shoot competition, the average monthly Li uptake of *F. pratensis* was 79 % (1994) and 74 % (1995) lower than that of *D. glomerata*.

In interspecific shoot competition the root dry weight per tiller of *F. pratensis* was significantly lower than that of *D. glomerata* in 1995 (Fig. 22B). However, as at soil depths of 0 to 0.12 m, the generally lower SAR of *F. pratensis* (Fig. 22C) was more relevant for the generally lower Li uptake than were the differences in root dry weight.
Figure 22: Seasonal change in lithium uptake per tiller from 0.30 m soil depth (A), root dry weight per tiller in 0.24 to 0.36 m soil depth (B), and specific absorption rate for Li in 0.24 - 0.36 m soil depth (C) of Festuca pratensis (▼, ▲) and Dactylis glomerata (●, ○) in intraspecific (▼, ●), and interspecific (▲, ○) shoot competition over two growing seasons. Mean values and standard errors (I) are shown.
5 DISCUSSION

5.1 Seasonal variation in canopy structure and its relation to shoot competitive ability

The total plant weight of *F. pratensis* in intraspecific shoot competition was lower than that of *D. glomerata* in 1994 but equal or higher to that of *D. glomerata* in 1995 (Fig. 12A). In interspecific shoot competition, the total plant weight of *F. pratensis* was strongly reduced, whereas *D. glomerata* increased its plant weight (Fig. 12B). This different response in mixture led to an overall decrease in the shoot competitive ability of *F. pratensis* relative to *D. glomerata* during the two growing seasons, more or less independent of the total plant dry weight in intraspecific shoot competition (Fig. 12C).

Carlen (1994) reported a progressive decline in the shoot competitive ability of *F. pratensis* relative to *D. glomerata*. In contrast, the root competitive ability of *F. pratensis* was similar to that of *D. glomerata* during spring and autumn but lower during summer. Our results support his conclusion that a low shoot competitive ability makes *F. pratensis* a weaker overall competitor as compared to companion grasses such as *D. glomerata*. In contrast to the results of Carlen (1994), the shoot competitive ability of *F. pratensis* changed with season, being comparatively high in spring and autumn but decreasing during summer (Fig. 12C). This seasonal pattern of shoot competitive ability of *F. pratensis* was closely related to its relative leaf area proportion in the upper canopy layers of the mixtures (Fig. 18). In interspecific shoot competition, *F. pratensis* accumulated a similar or higher leaf area than *D. glomerata* in the upper canopy layers during the first growth cycle and in autumn. In contrast, *F. pratensis* had no leaves or only a very low leaf area density in the upper canopy layers during summer. These differences in leaf area distribution in interspecific shoot competition reduced the light interception of *F. pratensis* during summer of both years as compared to its light interception intraspecific shoot competition, while the light interception of *D. glomerata* increased. As will be shown, the lower leaf area of
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*F. pratensis* in the upper canopy layers was mainly a consequence of its shorter leaves (Fig. 46, page 153).

The ability of a plant to place foliage in the upper, well-lit canopy layers is an important structural trait in competition for light (Berendse 1989; Akey, Jurik & Dekker 1990; Holt 1995). Differences in plant height are often more important than differences in the physiological characteristics of individual leaves (Caldwell 1987; Barnes et al. 1988; Holt 1995). In contrast, Teughels et al. (1995) argue that a greater total leaf area makes *Lolium perenne* the better competitor for light than *Festuca arundinacea*, even when canopy height and vertical leaf area distribution are similar. *F. pratensis*, the weaker shoot competitor, produced a lower total leaf area in interspecific shoot competition throughout most of the growing season and was additionally overtopped by *D. glomerata* from June to September. In growth chamber experiments, the rate of photosynthesis per leaf area of *F. pratensis* was higher than that of *Lolium multiflorum* (Bühring 1990), and its NAR was higher than that of *D. glomerata* (Fig. 1, page 30). Consequently, the photosynthetic capacity of individual leaves of *F. pratensis* is rather higher as compared to *D. glomerata*. Apparently, shading due to overtopping by *D. glomerata* during summer, was the major cause of the decline in the shoot competitive ability of *F. pratensis* relative to *D. glomerata*.

In an intensively defoliated grassland, as in this experiment, the low leaf area of *F. pratensis* in the upper canopy layers during the vegetative phase might be the consequence of a lower regrowth rate after defoliation. However, the ability of *F. pratensis* to extend a high proportion of leaf area to upper canopy layers might also be limited by a lower rate of leaf elongation or by differences in leaf attributes. In addition, the parameter that enabled *D. glomerata* to overtop *F. pratensis* probably changed with the growing season and year. Thus, in 1994 and 1995, different parameters or combinations of parameters might have limited the shoot competitive ability of *F. pratensis*, despite the comparable decline in competitive ability in both years.

In 1994, a lower regrowth rate probably restricted the shoot competitive ability of *F. pratensis* considerably. It will be shown that this was related to a higher proportion of reproductive tillers, which led to a lower proportion of elongating
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leaves during the second regrowth relative to *D. glomerata* (Fig. 27, page 107). Other possible factors which may have hindered the regrowth of *F. pratensis* in intraspecific shoot competition are the lower stubble dry weight (Fig. 13) and the lower content of water soluble carbohydrates (Fig. 20).

In 1995 differences in leaf elongation and leaf attributes of the two species may have been more important, because differences in stubble weight and content of water soluble carbohydrates in intraspecific shoot competition were negligible. The lower leaf elongation rate of *F. pratensis* as compared to *D. glomerata* might be a consequence of the high dry matter costs per unit leaf area due to the lower specific leaf area (Fig. 6, page 37). Other important limitations of the shoot competitive ability of *F. pratensis* were probably differences in the seasonal pattern of biomass allocation (Chapter 5.3) or a reduced regrowth rate due to the effects of shoot competition (Chapter 5.4).

5.2 Lower root activity of *F. pratensis*

The seasonal root activity pattern of *F. pratensis* and *D. glomerata* was measured with the non-radioactive tracers Rb and Li, as an indication of the pattern of resource acquisition in different soil layers. Measures of root activity have the advantage that they also reflect other root parameters, such as age, composition and physiological status of the roots as opposed to root dry weight and root distribution (Tofinga & Snaydon 1992).

The root activity of *F. pratensis* at soil depths of 0 to 0.12 m and 0.24 to 0.36 m was generally tremendously lower than that of *D. glomerata* and was only slightly affected by interspecific shoot competition. In intraspecific shoot competition, the average monthly marker uptake of *F. pratensis* at 0 to 0.12 m was 59% (1994) and 69% (1995) lower than that of *D. glomerata* (Fig. 21A) and even 79% (1994) and 74% (1995) lower in soil layers from 0.24 to 0.36 m (Fig. 22A). These findings are in agreement with the view of Grime (1979) who states that species which are superior competitors for light are also superior in acquiring below-ground resources.
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Differences in marker uptake were highest during the reproductive phase in spring. During the vegetative phase, differences increased to a maximum from July to August and then decreased again. Independent of soil depth, the generally lower root activity of *F. pratensis* was caused mainly by a consistently lower specific absorption rate (SAR) for Rb (Fig. 21C) and Li (Fig. 22C). Compared to species specific differences in SAR, differences in root dry weight per tiller were less important (Figs 21B & 22B). A constantly low SAR of *F. pratensis* was also the major cause of the lower Rb and Li uptake of *F. pratensis* during summer.

Mineral nutrients and water are commonly limiting factors in competition for below-ground resources (Donald 1963). Since the focus of this experiment was on shoot competition, our experimental design excluded interspecific root competition. In addition, competition for water was offset by irrigation, and nutrients were in ample supply. Since interspecific root competition was excluded, differences in the acquisition rate of resources by the roots were probably less important for the decreasing shoot competitive ability of *F. pratensis* as compared to the differences in shoot attributes. This situation changes when a species has to compete for above- and below-ground resources in permanent grassland. In the field, soil resources are often supplied in intervals due to sporadic rainfall and changes in temperature as well as effects of moisture on microbial activity. Species with a rapid and high acquisition of resources may have competitive advantages in root competition (Grime 1977; Goldberg 1990). Differences in root activity may be important for competitive success during summer when water may be in short supply. *F. pratensis* is known for a decreasing root competitive ability relative to *D. glomerata* during summer (Carlen 1994). The low root activity of *F. pratensis* found in the present study might be the pivotal trait responsible for this decline in root competitive ability of *F. pratensis* during summer.

After defoliation, root growth, root respiration, and nutrient absorption of grasses are inhibited (Richards 1993). Compared to *D. glomerata*, root growth of *F. pratensis* was inhibited for a longer period during regrowth at non-limiting nutrient supply (Fig. 2, page 32). A longer delay of root growth and root activity after defoliation might be responsible for the decreasing root competitive ability
II Seasonal variation of shoot competition

of *F. pratensis* during summer. The root activity and resource acquisition of *F. pratensis* and *D. glomerata* during regrowth after defoliation should be investigated further (Part III).

5.3 Seasonal variation in tillering and biomass allocation in intraspecific shoot competition

Biomass allocation is the result of the flow of assimilates from source organs to the competing sinks in different plant parts. However, source and sinks within a plant are not independent; for example, the use of sucrose by sinks will, in turn, affect the activity of source leaves (Farrar 1996). The biomass allocation to a particular sink depends, therefore, on the interaction of that sink with the rest of the plant. Thus, the seasonal pattern of biomass allocation of *F. pratensis* and *D. glomerata* to above- and below-ground plant parts mainly reflected the sink of a particular plant part in relation to the sinks of other plant parts.

The biomass allocation of *F. pratensis* to the shoot was higher as compared to *D. glomerata* during periods of relatively high shoot competitive ability in spring and autumn. During periods of low shoot competitive ability in summer, however, *F. pratensis* allocated the largest part of its dry matter to the roots in intraspecific shoot competition, but, relative to *D. glomerata*, considerably less dry matter to harvested plant parts and stubbles (Fig. 13). The greater biomass allocation of *F. pratensis* to the roots resulted in a consistently higher total root dry weight but was also accompanied by a generally much lower specific root activity relative to *D. glomerata* independent of soil depth (Figs 21 & 22). Contrary to the low biomass allocation to the shoot during summer, *F. pratensis* increased its tiller number in both years (Fig. 19). In contrast, the tiller number of *D. glomerata* decreased during summer despite the high biomass allocation to the shoot. This different seasonal pattern of tillering in intraspecific shoot competition resulted in, on average, 22 tillers per plant of *F. pratensis* during the vegetative phase in 1995 as compared to 11 tillers per plant of *D. glomerata*. Nevertheless the transmission of PPFD through the canopy remained high in *F. pratensis* swards as compared to *D. glomerata* swards. Despite its higher tiller
number, the light interception of *F. pratensis* 0.12 m above the soil surface was still lower (81%) relative to *D. glomerata* (91%) (Fig. 18). Consequently, self-shading due to differences in canopy structure during summer always occurred to a lesser extent in *F. pratensis* than in *D. glomerata*, independent of tiller number. The differences in self-shading between the two species in intraspecific shoot competition affected not only the light quantity, but also the light quality at the tiller bases. This in turn was probably one of the main determinants of the seasonal response of tillering and biomass allocation during the vegetative phase.

In *F. pratensis* swards, the higher light intensity and, probably also the higher red:far red ratio at the tiller bases in intraspecific shoot competition during summer enhanced its tillering. Self-shading remained low, and thus its shoot sink did not increase as compared to the other sinks. Consequently, a relatively high proportion of assimilates was allocated to the roots. Therefore, the low biomass allocation of *F. pratensis* to the shoot in intraspecific shoot competition was probably the result of a low sink due to differences in canopy structure and leaf attributes. On the other hand, it might also be related to a generally higher sink of the roots due to the low root activity relative to *D. glomerata*.

In *D. glomerata* swards, the tiller number decreased, probably due to the lower light intensity and lower red:far red ratio at the tiller bases. In contrast to *F. pratensis*, its self-shading and, consequently, its shoot sink remained high. Consequently, a relatively high proportion of assimilates was allocated to the shoot.

### 5.4 Different response of tillering and biomass allocation to interspecific shoot competition

The availability of above-ground and below-ground resources of a plant species can change in interspecific shoot competition as compared to intraspecific shoot competition. This change in resource availability can affect plant growth and biomass allocation. Relative to intraspecific shoot competition, the light availability in *F. pratensis* swards decreased in interspecific shoot competition from June to the middle of August because of shading and increased again until
October. In contrast, the light availability in *D. glomerata* swards increased in interspecific shoot competition during summer relative to intraspecific shoot competition. In mixture, only about 36 % of the PAR was intercepted by *F. pratensis* as compared to 64 % by *D. glomerata* at the end of regrowth from June to August in 1995 (Fig. 18).

*F. pratensis* responded to decreasing light availability during periods of strong competitive pressure from June to August with decreased tillering. *D. glomerata* responded to the higher light availability in interspecific shoot competition during summer with increased tillering (Fig. 19). This relation between light availability and tillering is a well-known phenomenon (Holt 1995). Reduced tillering with decreasing photon irradiance has been found by a number of researchers (Jelmini & Nosberger 1978; Allard, Nelson & Pallardy 1991; Zimmermann 1995). In line with the present study, Carlen (1994) found that *F. pratensis* had fewer tillers with decreasing light availability in shoot competition with *D. glomerata*, whereas *D. glomerata* increased its tiller number.

In contrast to the decreasing tiller number, *F. pratensis* in interspecific shoot competition increased its biomass allocation to harvested plant parts at the expense of WSC accumulation (Fig. 20) and biomass allocation to stubbles and roots (Fig. 16). *D. glomerata* responded to the higher light availability in interspecific shoot competition during summer with a lower biomass allocation to harvested plant parts but an increased biomass allocation to the roots and stubbles (Fig. 17). The specific response of biomass allocation of *F. pratensis* to interspecific shoot competition resulted in a 21 to 26 % higher shoot weight ratio in interspecific shoot competition from July to August in both years. In contrast, the shoot weight ratio of *D. glomerata* in interspecific shoot competition was lower by 11 to 17 %. This difference in the response of biomass allocation to interspecific shoot competition explains why shoot competition mainly affected root and stubble weight, while effects on shoot weight were weak (Fig. 13). Increased biomass allocation to the shoot in response to shading has been reported before (Jelmini & Nösberger 1978; Olff 1992; Holt 1995). In line with our study, Allard, Nelson, and Pallardy (1991) found reduced tillering and an increased shoot/root ratio in response to shading in *Festuca arundinacea*. These
II Seasonal variation of shoot competition

responses to shade were shown to be triggered by the low red:far red ratios under canopies (Holt 1995). Thus, both the increased biomass allocation to the shoot and the reduced tillering of *F. pratensis* were typical responses to changes in light quantity and quality imposed by shading. With a greater biomass allocation to leaves and leaf sheaths, *F. pratensis* probably tried to increase the light interception of existing tillers. However, despite its higher investments in harvested plant parts, its competitive ability decreased at the same time, since *D. glomerata* still reached much higher relative leaf area densities in the uppermost canopy layers in interspecific shoot competition. Thus, for *F. pratensis*, the weaker shoot competitor, the overall effects of the higher biomass allocation to harvested plant parts during summer were mainly negative, since a 21-26 % greater proportion of dry weight was removed by defoliation relative to intraspecific shoot competition. The regrowth rate of *F. pratensis* probably decreased in interspecific shoot competition due to the lower WSC content per tiller, the decreasing tiller number, and the decreasing stubble weight as compared to intraspecific shoot competition. The higher tiller number of *D. glomerata*, probably resulted in a better regrowth capacity after defoliation relative to intraspecific shoot competition and thus in a better shoot competitive ability. Therefore, depending on the season, a reduced regrowth rate of *F. pratensis* might also be the consequence of direct effects of shoot competition per se.

In full competition, the different response of biomass allocation to the roots in interspecific shoot competition would probably have affected the root competitive ability of both species, too. The decreasing biomass allocation to the roots, in combination with the low root activity, may have reduced the root competitive ability of *F. pratensis* as compared to *D. glomerata*. The higher biomass allocation of *D. glomerata* to the roots probably increased its ability to acquire soil resources in root competition. This supports the studies of Donalds (1958) and Carlen (1994) who found a positive interaction between root and shoot competition. Therefore, the competitive ability of *F. pratensis* in full competition would probably have been less than the sum of its shoot and root competitive ability.
5.5 Conclusions

_**F. pratensis**_ was a weaker shoot competitor than _D. glomerata_ which had little to do with its total dry weight production in intraspecific shoot competition. The shoot competitive ability of _F. pratensis_ changed considerably with season. It was relatively high during reproductive growth and in autumn. Despite this advantage, the shoot competitive ability of _F. pratensis_ decreased as a consequence of its lower leaf area proportion in the upper canopy layers during vegetative growth in summer.

_F. pratensis_, the weaker shoot competitor, typically allocated more biomass to the roots and had a low root activity, especially during summer. _D. glomerata_, the stronger shoot competitor, allocated more biomass to the stubbles, had a higher total WSC content, and generally showed a higher root activity.

Interspecific shoot competition affected plant growth and biomass allocation of the whole plant. _F. pratensis_ responded to shading with reduced tillering and a higher biomass allocation to harvested plant parts at the expense of WSC accumulation and biomass allocation to stubbles and roots, while the opposite was true of _D. glomerata_. The effects of the higher biomass allocation to the shoot were mainly negative for _F. pratensis_, because a greater proportion of dry weight was removed by defoliation than in intraspecific shoot competition. Additional experiments are necessary to add to our understanding of the parameters determining the shoot competitive ability of grasses in a frequently defoliated sward. The seasonal regrowth pattern of _F. pratensis_ and _D. glomerata_ and its consequences for shoot competitive ability should be investigated.
PART III:
THE RELATION BETWEEN PLANT ARCHITECTURE, BIOMASS ALLOCATION, AND REGROWTH OF FESTUCA PRATENSIS AND DACTYLIS GLOMERATA

1. SUMMARY

Inherent differences in regrowth rate can limit the persistence of a species in an intensively managed grass sward. Our objective was to compare the seasonal variation of regrowth of Festuca pratensis Huds. (Meadow fescue), a weak shoot competitor, relative to Dactylis glomerata (Orchard grass), a strong shoot competitor, in the field over two years. With fully destructive harvests the effects of season and regrowth on canopy architecture, biomass allocation, and the content of water soluble carbohydrates were assessed. The nutrient acquisition at soil depths of 0 to 0.12 m and 0.24 to 0.36 m was estimated during regrowth from the uptake of the non-radioactive tracers Rubidium and Lithium.

F. pratensis had a higher RGR during the reproductive growth cycle than D. glomerata due to a faster increase in LAR in April, a higher NAR and, in one year, a higher proportion of reproductive tillers. After the reproductive growth cycle, the lower proportion of vegetative tillers and, thus, remaining shoot meristems, strongly reduced the regrowth capacity of F. pratensis relative to D. glomerata.

During summer, when the plants were fully vegetative in the previous growth cycle, LAR of both species increased similarly for one to two weeks, since F. pratensis compensated for its generally lower SLA by a higher LWR. After this initial period, D. glomerata considerably increased its LAR relative to F. pratensis due to its higher SLA and a higher biomass allocation to the shoot. In addition, D. glomerata showed a generally higher RGRLA and a higher nutrient acquisition rate as compared to F. pratensis. In fully vegetative plants, the striking differences in canopy architecture, biomass allocation, and nutrient acquisition were probably more important determinants of shoot competitive ability than inherent differences in RGR.
2. INTRODUCTION

The proportion of *Festuca pratensis* (Meadow fescue), a valuable component of meadows and pastures in upland regions, has drastically decreased over the last century. Today, *F. pratensis* is found only in small proportions in extensively managed permanent grasslands. The intensification of grassland management is considered to be an important reason for the decreased competitive ability of *F. pratensis* as compared to other grasses (Mott 1982; Meister & Lehmann 1990). Indeed, *F. pratensis* is not very persistent when grown with *D. glomerata* (Orchard grass), a competitive companion grass under high management intensity (Gügler 1993; Carlen 1994). Experiments of Carlen (1994) demonstrated that a low shoot competitive ability usually limits the persistency of *F. pratensis* in highly fertile soils. In a previous study we analysed the effects of season and shoot competition on above- and below-ground plant traits of *F. pratensis* relative to *D. glomerata* as well as the consequences for shoot competitive ability in an intensively defoliated grassward (Part II). In this study shoot competitive ability of *F. pratensis* strongly changed with season. Despite a relatively high competitive ability during reproductive growth and in autumn, the shoot competitive ability of *F. pratensis* decreased due to the negative effects of a lower shoot competitive ability during vegetative growth in summer. This was caused by a lower leaf area proportion in the upper canopy layers in interspecific shoot competition and, thus, increased shading.

One of the major factors determining success in plant competition is the ability of a plant to extend leaves and roots in order to capture undepleted resources before they are consumed by neighbouring individuals (Grime 1979). A rapid replacement of photosynthetic tissue after defoliation can be important for competitive success in an intensively defoliated sward. Species often differ in their regrowth capacity due to inherent differences in their ability to regrow quickly, to re-establish foliage, and to convert carbon and nutrients into new photosynthetic tissue and other plant structures. In growth chamber experiments, *F. pratensis* showed a lower regrowth capacity than *D. glomerata*, mainly caused by a slower leaf area development after defoliation (Fig. 3, page 33). These results suggest that the shoot competitive ability of *F. pratensis* in more fertile
soils might be limited by an inherently lower regrowth capacity during the vegetative phase relative to companion grasses such as *D. glomerata*.

The rate of regrowth after defoliation is related to the content of reserves (Shread 1973) and to the photosynthetic activity of the residual plant parts (Davies 1974). Water soluble carbohydrates (WSC), mainly stored in the tiller bases, are commonly thought to be an important source of carbon for regrowth after defoliation of forage grasses (Smith 1973; Kigel 1980; Volenec 1985). In the field however, photosynthesis of the remaining leaf area and leaf sheaths (Booysen & Nelson 1975; Richards & Caldwell 1985; Danckwerts 1993) or differences in meristematic activity (Davies 1988; Bassetti 1989; Richards 1993) are often more important for regrowth than differences in carbohydrate reserves. In addition, the factors or the factorial combinations limiting regrowth and shoot competitive ability will probably change with season, related, for example, to differences in the species-specific response to environmental conditions.

The purpose of this study was to analyse the seasonal variation of regrowth of *F. pratensis* and *D. glomerata* in intraspecific shoot competition in an intensively defoliated grass sward and its effects on the whole plant.

Our goals were: (1) to determine whether there are inherent differences in the regrowth rate of the two species, (2) to assess the effects of season and regrowth on shoot attributes, biomass allocation, reserve accumulation, and root activity and (3) to assess the most important parameters limiting regrowth depending on season.

The study showed that there seem to be two main factor complexes limiting the competitive ability of *F. pratensis*. Depending on season and year these are (i) a reduced regrowth capacity due to a lower proportion of active shoot meristems after the reproductive growth cycle and (ii) differences in leaf attributes and biomass allocation to shoot and roots.
3. MATERIALS AND METHODS

3.1 Experimental method and treatments

A field experiment on shoot competition was carried out at the research station of the Swiss Federal Institute of Technology in Eschikon, near Zurich, Switzerland (550 m above sea level.), from October 1993 to October 1995. The experiment was a completely randomised block with four replications (four forcing beds of 10 x 1.45 m). Each forcing bed consisted of two swards (2.56 x 1.38 m) with either Festucapratensis (Meadow fescue) or Dactylis glomerata (Orchard grass) in intraspecific shoot competition.

Root competition was separated using the experimental technique of Donald (1963), modified for fully destructive sequential harvesting. The soil of the forcing beds was removed and polystyrol partitions, held together by thread posts, were inserted. The partitions divided the soil part of the plots into 36 compartments of 1.2 x 0.06 x 0.45 m. The compartments were caulked of each other to prevent the intermingling of roots. Two boxes (0.60 x 0.40 x 0.45 m) were installed at the front of each plot to be used as movable borders. After inserting the polystyrol partitions and the movable borders, the forcing beds were carefully refilled with a 80/20 volume percent mixture of strained fertile soil and sand (0 - 3 mm) to a height of 0.45 m.

3.2 Experimental set-up, establishment and growth conditions

Seedlings of F. pratensis Huds. cv. Predix (RAC, CH) and D. glomerata L. cv. Baraula (Barenbrug, NL) were grown in quick-pots in the glasshouse for 35 days. Selected plants were transplanted into the forcing beds outdoors from 1 to 6 October 1993. Each species was planted row-wise into the compartments at a density of 278 plants m\(^2\) (planting distance 0.06 x 0.06 m). Each row consisted of 23 plants, the innermost eight of which were used for analysis. The rest of the plants served as a border. This gave a border of 0.48 m (south side) and 0.42 m
(north side), respectively, along the lateral sides of the plots. There was also a border of 0.40 m along the front side of each plot.

In March 1994 and 1995, all treatments were supplied with 5 g P/m², 26 g K₂O/m², and 3 g Mg/m² dissolved in water. Nitrogen was applied in spring before growth started and one day after each defoliation, in a solution of NH₄NO₃ at a rate of 32 g N m⁻² year⁻¹. The plots were irrigated during summer so that water did not limit growth. Unwanted plant species were removed throughout the experiment.

3.3 Sequential harvesting

The swards were defoliated six times per growing season on 20 May, 21 June, 21 July, 18 August, 15 September, 18 October 1994 and on 17 May, 21 June, 20 July, 22 August, 18 September, and 19 October 1995 (Table 3).

1994:

<table>
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<th>Days after def.</th>
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<th>Growth analysis</th>
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<tbody>
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<tr>
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<td>20 25 31 08 21</td>
<td>21 26 02 09 18</td>
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<tr>
<td>15 18</td>
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1995:

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<th>Growth analysis</th>
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<tr>
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<tr>
<td>04 18 01 09 17 23 29 07 21</td>
<td>20 26 02 09 22</td>
<td>18 19</td>
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Table 3: Dates of fully destructive sequential harvests to analyse the seasonal variation in regrowth of *F. pratensis* and *D. glomerata* in intraspecific shoot competition in 1994 and 1995. The swards were grown under field conditions and defoliated six times per growing season (\( \downarrow \)). Growth analyses were made to determine the seasonal variation in regrowth after defoliation (\( \downarrow \)). In 1994, vegetative regrowth after the first and the third defoliations were analysed. In 1995, the reproductive growth cycle in spring, its relation to vegetative regrowth after the first defoliation, and vegetative regrowth after the third defoliation were analysed.
The swards were in the reproductive stage at the first defoliation and in the vegetative stage at subsequent defoliation in both years. Fully destructive sequential harvests were made to determine the seasonal variation of regrowth after defoliation. In 1994, vegetative regrowth after the first and the third defoliation was analysed. In 1995, we analysed the reproductive growth cycle in spring, its relation to vegetative regrowth after the first defoliation and vegetative regrowth after the third defoliation. The reproductive growth cycle in 1995 was analysed with sequential harvests on 3 April, 18 April, 1 May, 9 May, and on 17 May. For growth analysis during the vegetative phase, sequential harvests were made at the day of defoliation (0) and after 5 to 6, 11 to 13, 19 to 21 and 28 to 35 days of regrowth.

At each harvest one entire plant per plot was harvested fully destructively. A new sampling technique was used for sequential harvesting and stratified clipping. The technique allowed precise and efficient harvesting and stratified clipping of the whole plants, independent of season and weather. Undisturbed plant rows were made accessible by removing the boxes with the border plants at the front of the swards and the lateral polystyrol partition of the root compartment. A specially designed plate was pressed vertically against the root compartment of the selected plant row. The root compartment of the plant row was loosened and the plant row placed on the plate. The plate was slowly turned from a vertical to a horizontal position and the plant row removed from the sward. The shoots of the plant row were gently pressed. The press (0.96 x 0.6 m) consisted of a central element (0.48 x 0.6 m) and two lateral elements (0.24 x 0.6 m) all of which could be taken apart. The central element could again be separated (starting at the top: two elements 0.48 x 0.15 m, one element 0.48 x 0.12 m, one element 0.48 x 0.08 m, and two elements 0.48 x 0.05 m). After removing the lateral elements of the press, the shoot and stubble fractions of the border plants were cut away and eliminated. The shoots of the eight innermost plants (0.48 x 0.6 m) remained under the central part of the press. A template was used to determine the corresponding root volume of the sample plants and the root volume of the border plants was removed. The remaining plants under the press were used for stratified clipping and further investigations. Using the template, the root compartment of
the sample was divided into three layers at depths of 0-0.12 m, 0.12-0.24 m, and 0.24-0.36 m and removed. Plants were defoliated 0.05 m above the root system to give the stubble fraction. Stratified clipping of the shoots took place, starting at the top of the sample plants, by removing element per element of the press. Depending of season and time of regrowth biomass in up to seven canopy layers (0.80-0.65, 0.65-0.50, 0.50-0.35, 0.35-0.23, 0.23-0.15, 0.15-0.10, 0.10-0.05 m above-ground) was harvested.

After the sequential harvests, thread posts were cut back to the next compartment secured by screws, the boxes with the border plants reinstalled and the rest of the swards defoliated to 0.05 m above the soil surface.

3.4 Plant measurements

The biomass of each canopy layer was separated to give leaf lamina and leaf sheaths and the leaf number counted. Leaf area and leaf length was measured with a photoelectric meter (Model Li-3000 A; Li-Cor Inc. Lincoln, NE, USA). Stubbles were washed, senescent tillers removed, and the tiller number determined. A tiller was included if it was longer than 5 cm. The proportion of reproductive tillers at the first defoliation was determined as the inverse of the tiller number with elongating leaves after five to six days of second regrowth relative to the total tiller number. A subsample of 40% of the stubble fraction was separated into senescent leaf sheaths and green plant material for later determination of the content of water soluble carbohydrates and calculation of the total stubble weight. The content of water soluble carbohydrates was determined as described before (Chapter 3.7, Part II).

Roots were washed out by rinsing the soil samples on a sieve with a mesh gauge of 1.25 mm. All samples were dried at 65°C for 48 hours and the dry weight determined.
3.5 Measurement of light transmission

The photosynthetic active photon flux density (PPFD) in different canopy layers was measured at the harvests on 1, 9 and 17 May 1995, to assess the changes in the vertical distribution of PPFD during the reproductive growth cycle. PPFD was determined by means of a Decagon Sunfleck Ceptometer (Decagon Devices Inc., USA) with a light sensitive area of 800 x 10 mm, horizontally placed into the canopy 0.12, 0.19, 0.29 m and 0.42 m above-ground. The relative PPFD was calculated against a reference PPFD above the canopy to give the light transmission (T) in the canopy.

3.7 Root activity

Rubidium (Rb) and lithium (Li) served as non-radioactive tracers to determine the root activity at soil depths of 0.06 and 0.30 m. Rb and Li are taken up in a similar manner as potassium, are non-toxic in concentrations that are already determinable, are not easily leached, and are in the soil of low natural concentration (Fitter 1986). In this experiment, the natural concentration varied between 6 and 24 ppm Rb and between 2 and 16 ppm Li for both grasses. Root activity was measured as Rb and Li uptake per shoot. The 14 innermost plants per root compartment were marked with Rb and Li tracer solutions. The tracer solutions were injected into the soil at 13 application points per root compartment midway between two plants. A syringe which refilled automatically (Socorex ISBA S.A., CH) was used to inject 4 ml tracer solution per application point at soil depth of 0.06 m (40 mg Rb as RbCl diluted in water) and 0.30 m (40 mg Li as LiCl diluted in water). In spring (20 April 1994 and 21 April 1995) and on the first day of regrowth after the last defoliation, the compartments for sequential harvests, after 5 to 6 days, 11 to 13 days, 19 to 21 days, and 28 to 35 days of regrowth, were marked. A random sample of 8 to 10 tillers of the four innermost plants, defoliated at ground level, was used for the analyses. After senescent tissues were removed, the plant material was dried at 65 °C for 48 h.
All analyses were performed in the laboratory of Prof. Frossard at the Institute of Plant Sciences in Lindau-Eschikon, Switzerland. A subsample of approximately 250 mg was ashed at 540 °C for six hours. The ashes were dissolved in 2 ml HCl (20 % v/v) for 15 minutes at 70 °C and transferred to 50 ml flasks to which 1 ml of CsCl solution (80 g CsCl/l) was added. The volume was adjusted to 50 ml with distilled water and filtered (meshwidth 0.8 μm). The Rb content of the filtrate was determined by an atomic absorption spectrophotometer (Perkin-Elmer 5000) and Li by emission (ICP, Model Varian Liberty 200).

3.8 Data analysis

Growth analysis calculations were made according to the functional approach (Hunt 1982) using a PC edition (HP curves, Bristol, UK. Hunt & Parsons 1994) of the computer program of Hunt & Parsons (1974). Polynomials of varying degree were fitted to Ln-transformed total dry weight per plant (W) and Ln-transformed leaf area per plant (LA) versus days after defoliation (tₐ) by the least square method. The following plant growth functions were used: relative growth rate (RGR= 1/W x dW/dt), RGR of leaf area (RGRLA= 1/LA x dLA/dt), and the net assimilation rate (NAR= 1/LA x dW/dt). Non-transformed data were used to calculate the leaf area ratio (LAR= LA/W), the specific leaf area (SLA= leaf area per leaf weight), and the leaf weight ratio (LWR= leaf weight per total plant weight). For growth analysis after the defoliation on 21 July 1994, two replicates of F. pratensis were excluded, since the plants were infected by root aphids (Geoica setulosa, Pass., 1860).

All calculations not computed by the Hunt and Parsons computer program were made with the SAS statistical package (Statistical Analyses System, Version 6.10, SAS Institute Inc., Cary, North Carolina, USA). Data were Ln-transformed before the analysis of variance if variances were not distributed normally and not homogeneous. Analysis of variance and standard error of the means (s.e.) were calculated according to the GLM procedure.
4. RESULTS

4.1 The relation between reproductive development and regrowth after the first defoliation

4.1.1 Analysis of the reproductive growth cycle

The stubble dry weight of *F. pratensis* swards was 35 % lower than that of *D. glomerata* swards on 3 April 1995 (Table 4). This weight difference was mainly the result of the lower stubble weight of *F. pratensis* in October 1994, because the loss of stubble weight during the winter (24 %) was similar to that of *D. glomerata* (26 %).

Table 4: Impact of overwintering on different plant traits of *Festuca pratensis* and *Dactylis glomerata* in intraspecific shoot competition. Stubble dry weight, content and percentage of water soluble carbohydrate (WSC) of stubbles, as well as number of tillers per plant and total leaf area on 3 (18) April 1995 are compared to values on 18 October 1994. Mean values and standard errors (s.e.) are shown.

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<th><em>D. glomerata</em></th>
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<td>79</td>
<td>226</td>
<td>28.0</td>
</tr>
<tr>
<td>WSC percentage of stubbles</td>
<td>18 Oct. 94</td>
<td>34.4</td>
<td>36.9</td>
<td>2.2</td>
</tr>
<tr>
<td></td>
<td>03 Apr. 95</td>
<td>10.1</td>
<td>18.7</td>
<td>1.1</td>
</tr>
<tr>
<td>Number of tillers</td>
<td>18 Oct. 94</td>
<td>14.0</td>
<td>13.3</td>
<td>0.8</td>
</tr>
<tr>
<td></td>
<td>18 Apr. 95</td>
<td>32.9</td>
<td>25.3</td>
<td>3.1</td>
</tr>
<tr>
<td>Leaf area</td>
<td>03 Apr. 95</td>
<td>35.2</td>
<td>48.3</td>
<td>4.9</td>
</tr>
</tbody>
</table>
The percentage of water soluble carbohydrates (WSC) in stubbles in *F. pratensis* (10.1 %) was substantially lower than in *D. glomerata* (18.7 %) on the 3 April 1995 but similar for both species on 18 October 1994. In combination with its lower stubble dry weight, the WSC content of *F. pratensis* was dramatically lower (79 mg) than that of *D. glomerata* (226 mg) on 3 April 1995.

The number of tillers per plant increased strongly from October 1994 to the 18 of April 1995 and was similar for both species. The total leaf area per plant was with 35.2 cm² for *F. pratensis* and 48.3 cm² for *D. glomerata* on 3 April 1995 already quite high but did not differ significantly.

Ln-transformed total dry weight in intraspecific shoot competition of both species constantly increased during the reproductive growth cycle in spring 1995 (Fig. 23). At the first estimation on 3 April *F. pratensis* had a 20 % lower total dry weight than *D. glomerata*. At the first defoliation on 17 May, however, both species reached a similar total dry weight due to the considerably higher RGR of *F. pratensis* (Figs 23A & B). Until the beginning of May, the higher RGR of *F. pratensis* was to the same extent caused by its higher LAR and NAR as compared to *D. glomerata*, thereafter mainly by its higher NAR (Figs 23C & D). The higher LAR of *F. pratensis* until the beginning of May was the result of a generally higher LWR (Fig. 23F). Towards the end of the growth cycle, *D. glomerata* compensated its lower LWR by a higher SLA (Fig. 23E).

No significant differences in leaf area development between the two species were observed (Fig. 23G). RGRLA of both species increased until the end of April to a maximum of approximately 0.06 cm² cm⁻² day⁻¹ and decreased again towards the first defoliation on 17 May (Fig. 23H). RGRLA of *F. pratensis* was higher during the first half of April, thus, compensating for its slightly lower leaf area at the first estimation but comparable to that of *D. glomerata* thereafter.
Figure 23: Analysis of the reproductive growth cycle of *Festuca pratensis* (▼, ——) and *Dactylis glomerata* (●, ——) in intraspecific shoot competition in spring 1995. Ln-transformed dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), leaf weight ratio (F), Ln-transformed leaf area (G), and relative leaf growth rate (H) are shown. Each data point is the mean of four replicates. A polynomial was fitted through the original data points in (A, C, & G). I indicates the standard errors of the means.
Canopy height gradually increased during the reproductive growth cycle in spring 1995 to a height of 0.50 to 0.65 m above-ground at the first defoliation on 17 May (Fig. 24). The vertical leaf area distribution of the two grasses in intraspecific shoot competition was comparable at all harvests. Therefore, no species-specific differences in the change of canopy structure were found during the period from the middle of April to the middle of May. In contrast, the transmission of PPFD trough the two swards differed. It was the same for both species 0.29 m above-ground at the harvests on 1 and 9 May but higher for *F. pratensis* at 0.12 m and 0.19 m above-ground. At the end of the growth cycle, the transmission of PPFD in *F. pratensis* swards in the uppermost canopy layers was considerably higher than in *D. glomerata* swards.

![Figure 24: Changes in vertical distribution of leaf area density of Festuca pratensis (2) and Dactylis glomerata (1) in intraspecific shoot competition from 18 April 1995 until the first defoliation on 17 May 1995. The curves represent the transmission of photosynthetic photon flux density. Mean values and standard errors (1) are shown.](image)
4.1.2 Yield at the first defoliation

The shoot yield per plant of *F. pratensis* at the first defoliation was slightly, but not significantly, higher than that of *D. glomerata* in both years (Table 5). Averaged over both species, shoot yield was 15% lower in 1995 than in 1994.

The total dry weight per plant of *F. pratensis* was significantly lower in 1994 but similar to that of *D. glomerata* in 1995. Both grasses strongly increased their tiller number from spring 1994 to spring 1995. On average, the tiller number per plant of *F. pratensis* was nearly 60% higher than that of *D. glomerata*.

In 1994, *F. pratensis* produced a distinctly higher proportion of reproductive tillers (74.7%) than *D. glomerata* (52.4%). In spring 1995, however, the proportion of reproductive tillers of *F. pratensis* (25.5%) and *D. glomerata* (26.3%) was lower and in the same range.

Table 5: Shoot yield, total plant dry weight, tiller number per plant, and proportion of reproductive tillers per plant of *Festuca pratensis* and *Dactylis glomerata* in intra-specific shoot competition at the first defoliation on 20 May 1994 and on 17 May 1995. Mean values and standard error (s.e.) are shown.

<table>
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<tr>
<th>Parameters</th>
<th>Year</th>
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<th><em>D. glomerata</em></th>
<th>s.e.</th>
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</thead>
<tbody>
<tr>
<td>Shoot yield (mg dw plant⁻¹)</td>
<td>1994</td>
<td>2042</td>
<td>1993</td>
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<tr>
<td></td>
<td>1995</td>
<td>1780</td>
<td>1647</td>
<td>95.6</td>
</tr>
<tr>
<td>Total plant dry weight (mg plant⁻¹)</td>
<td>1994</td>
<td>3531</td>
<td>3886</td>
<td>112</td>
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<tr>
<td></td>
<td>1995</td>
<td>3965</td>
<td>3965</td>
<td>200</td>
</tr>
<tr>
<td>Number of tillers (plant⁻¹)</td>
<td>1994</td>
<td>12.9</td>
<td>7.8</td>
<td>0.65</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>29.4</td>
<td>19.4</td>
<td>1.70</td>
</tr>
<tr>
<td>Proportion of reproductive tillers (%)</td>
<td>1994</td>
<td>74.7</td>
<td>52.4</td>
<td>0.04</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>25.5</td>
<td>26.3</td>
<td>4.00</td>
</tr>
</tbody>
</table>

4.1.3 Residual plant parts

Averaged over both species a lower proportion of total dry weight was removed by defoliation in 1995 than in 1994, probably due in part to the higher proportion
of reproductive tillers in 1994 (Table 6). After defoliation, the remaining proportion of total plant dry weight of *F. pratensis* was significantly lower in 1994 and slightly lower in 1995. The remaining stubble dry weight per plant in *F. pratensis* swards after defoliation was much lower in both years than in *D. glomerata* swards. In contrast, root dry weight of both grasses was similar.

No residual leaf area was found after the reproductive growth cycle in 1994. In 1995, the remaining leaf area of *F. pratensis* (1.5 cm²) and *D. glomerata* (2.1 cm²) after the first defoliation was very low.

Averaged over both species, the WSC content in stubbles was nearly 60 % lower in 1994 than in 1995. The WSC content in stubbles of *F. pratensis* (47 mg) was much lower than that of *D. glomerata* (105 mg) in 1994, but comparable for both species in 1995. The WSC content of roots was similar for both grasses in 1994 but in 1995 significantly higher in *F. pratensis* than in *D. glomerata*.

**Table 6:** Remaining proportion of total plant dry weight, dry weight of stubbles and roots, residual leaf area, and the content of water soluble carbohydrates (WSC) of stubbles and roots per plant of *Festuca pratensis* and *Dactylis glomerata* in intraspecific shoot competition at the first defoliation on 20 May 1994 and on 17 May 1995. Mean values and standard errors (s.e.) are shown.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>Year</th>
<th><em>F. pratensis</em></th>
<th><em>D. glomerata</em></th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Remaining proportion of total plant dry weight (%)</td>
<td>1994</td>
<td>42</td>
<td>49</td>
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<td></td>
<td>1995</td>
<td>55</td>
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<td>Stubble dry weight (mg plant⁻¹)</td>
<td>1994</td>
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<td>51</td>
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<tr>
<td></td>
<td>1995</td>
<td>1036</td>
<td>1311</td>
<td>42</td>
</tr>
<tr>
<td>Root dry weight (mg plant⁻¹)</td>
<td>1994</td>
<td>847</td>
<td>904</td>
<td>41</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>1149</td>
<td>1007</td>
<td>103</td>
</tr>
<tr>
<td>Residual leaf area (cm² plant⁻¹)</td>
<td>1994</td>
<td>0.0</td>
<td>0.0</td>
<td>-</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>1.5</td>
<td>2.1</td>
<td>0.2</td>
</tr>
<tr>
<td>WSC content of stubbles (mg plant⁻¹)</td>
<td>1994</td>
<td>47</td>
<td>105</td>
<td>12</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>156</td>
<td>205</td>
<td>20</td>
</tr>
<tr>
<td>WSC content of roots (mg plant⁻¹)</td>
<td>1994</td>
<td>22</td>
<td>19</td>
<td>2.7</td>
</tr>
<tr>
<td></td>
<td>1995</td>
<td>45</td>
<td>26</td>
<td>4.3</td>
</tr>
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</table>
4.1.4 Consequences of reproductive development for regrowth after the first defoliation

The Ln-transformed total dry weight decreased for both species after the first defoliation in spring 1994, reached a minimum and increased again during the second half of the regrowth period (Fig. 25A). For *F. pratensis* this period of dry weight loss after defoliation with a negative RGR lasted about 18 days, leading to a total dry weight loss of about 12 % as compared to initial values (Figs 25A & B). Relative to *F. pratensis*, regrowth of *D. glomerata* was considerably faster. Already 10 days after defoliation *D. glomerata* again reached a positive RGR with a total dry weight loss of only about 9 % as compared to initial values. Averaged over the whole regrowth period, the RGR of *F. pratensis* was -0.004 mg mg⁻¹ day⁻¹ versus 0.003 mg mg⁻¹ day⁻¹ for *D. glomerata*. Compared to initial dry weights, these differences in RGR led to a 6% overall dry weight loss of *F. pratensis* at the second defoliation relative to a 18 % dry weight gain of *D. glomerata*. These differences in dry weight accumulation resulted in a 59 % higher total plant dry weight of *D. glomerata* as compared to *F. pratensis* at the second defoliation.

During the first two weeks after defoliation, part of the lower RGR of *F. pratensis* could be explained by a lower NAR (Fig. 25D). Thereafter, differences in LAR became much more important (Fig. 25C) in explaining the interspecific differences in relative growth rate.

For both grasses, SLA was highest at the beginning of regrowth and decreased thereafter (Fig. 25E). Averaged over all harvests, *F. pratensis* had a 18 % lower SLA than *D. glomerata*. Striking differences in SLA were found at the first sequential harvest, five days after defoliation, with 348 cm² g⁻¹ for *F. pratensis* and 510 cm² g⁻¹ for *D. glomerata*. Until approximately two weeks after defoliation, differences in LAR were mainly attributed to the lower SLA of *F. pratensis* and afterwards mainly to a lower LWR.
Figure 25: Ln-transformed total dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), and leaf weight ratio (F) of Festuca pratensis (▼, ▼) and Dactylis glomerata (●, ●) in intraspecific shoot competition during vegetative regrowth after the first defoliation on 20 May 1994. Each point is the mean of four replicates. A second-order polynomial was fitted through the Ln-transformed original dry weights in graph (A). I represents the standard errors for the fitted values in (A, B, C & D) and the standard errors of the means in (E & F).
Figure 26: Ln-transformed total dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), and leaf weight ratio (F) of Festuca pratensis (\(\text{\textbullet}\text{---}\)) and Dactylis glomerata (\(\text{\textbullet}\text{---}\)) in intraspecific shoot competition during vegetative regrowth after the first defoliation on 17 May 1995. A second-order polynomial was fitted through the Ln-transformed original dry weights in graph (A). I represents the standard errors for the fitted values in (A, B, C & D) and the standard errors of the means in (E & F).
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In contrast to 1994, only very few interspecific differences in the regrowth pattern of *F. pratensis* and *D. glomerata* after the first defoliation were found in 1995. Defoliation was again followed by a period of loss in total dry weight lasting 16 to 18 days for both species and an increase in total dry weight, thereafter (Fig. 26A). The RGR of both species showed a parallel increase during regrowth (Fig. 26B). Averaged over all harvests, the RGR of *F. pratensis* was slightly higher (-0.004 mg mg\(^{-1}\) day\(^{-1}\)) than that of *D. glomerata* (-0.006 mg mg\(^{-1}\) day\(^{-1}\)). During the first half of the regrowth period, LAR in *F. pratensis* was significantly higher and NAR slightly higher than in *D. glomerata* (Figs 26C & D). As in 1994, *F. pratensis* had, on average, a 18 % lower SLA but in contrast to 1994 a 25 % higher LWR than *D. glomerata* (Figs 26E & F).

4.1.5 Changes in leaf attributes during regrowth

After the first defoliation in 1994 with a high proportion of reproductive tillers, the refoliation in *F. pratensis* swards was clearly slower than in *D. glomerata* swards (Fig. 27). The slower leaf growth of *F. pratensis* as compared to *D. glomerata* led to 45 % lower total leaf area per plant already after five days of regrowth, resulting in a 67 % lower leaf area at the second defoliation (Fig. 27A). Differences in individual leaf size and average leaf number were mostly responsible for the differences in total leaf area, since RGRLA of both grasses was similar (Fig. 27B). Compared to *D. glomerata*, the average leaf size of *F. pratensis* was smaller, with dramatically increasing differences in average leaf size during the second half of regrowth (Fig. 27C).

During the first two weeks of regrowth, leaf length of both grasses increased similarly (Fig. 27E). Hence, the smaller leaves of *F. pratensis* were mainly the result of a smaller average leaf width (Fig. 27F). After two weeks, the average leaf length of *F. pratensis* remained constant at about 8 cm. In contrast, *D. glomerata* leaves continued to extend and reached an average length of 22 cm by the second defoliation. These increasing differences in average leaf length explained the lower average leaf size of *F. pratensis* during the second half of regrowth.
Figure 27: Ln-transformed leaf area (A), relative growth rate of leaf area (RGRLA) (B), average leaf size (C), leaf number per plant (D), average leaf length (E), and average leaf width (F) of Festuca pratensis (▼,---) and Dactylis glomerata (○,--–) in intraspecific shoot competition during regrowth after the first defoliation on 20 May 1994. Each point is the mean of four replicates. A second-order polynomial was fitted through the original Ln-transformed leaf area data points. I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).
In contrast to 1994, the increase in total leaf area per plant of *F. pratensis* was higher than that of *D. glomerata* during the first two weeks of the second regrowth in 1995 but slightly lower at the end of the regrowth period (Fig. 28A).

**Figure 28:** Ln-transformed leaf area (A), relative growth rate of leaf area (RGRLA) (B), average leaf size (C), leaf number per plant (D), average leaf length (E), and average leaf width (F) of *Festuca pratensis* (••••) and *Dactylis glomerata* (•,—) in intraspecific shoot competition during regrowth after the first defoliation on 17 May 1995. A third-order polynomial was fitted through the original Ln-transformed leaf area data points. I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).
During the first two weeks the major part of the higher leaf area of *F. pratensis* could be explained by a greater leaf number (Fig. 28D), which compensated for the lower average leaf width (Fig. 28F). During the second part of the regrowth period, the average leaf size of *F. pratensis* remained at a comparably low level, while *D. glomerata* strongly increased its leaf size (Fig. 28C), again mainly caused by differences in average leaf length (Fig. 28E). In contrast to 1994, the total area of both species did not differ significantly at the second defoliation, since *F. pratensis* nearly compensated for its lower leaf size by a strong increase in average leaf number per plant (Fig. 28D).

### 4.1.6 Changes in canopy structure during regrowth

The vertical distribution of leaf area in the canopies of vegetative *F. pratensis* and *D. glomerata* swards at the second defoliation was strongly affected by the increasing species-specific differences in leaf attributes during regrowth in both years. *F. pratensis* swards were relatively prostrate with a maximal height of 0.35 m and the highest leaf area density near ground (Figs 29A & C). *D. glomerata* swards were denser, relatively erect with leaves up to 0.50 m above the ground and, more leaves in higher strata (Figs 29B & D). In *D. glomerata* swards, 68% of the foliage produced between day 19 and 31 of regrowth in 1994 and 84% of the foliage produced after day 21 in 1995 were found in the strata between 0.15 and 0.50 m above-ground. In contrast, *F. pratensis* placed only 15% (1994) and 49 % (1995) of its foliage produced during the same period into the strata between 0.15 and 0.50 m and the rest of its foliage into the lowest canopy strata.
4.1.8 Water soluble carbohydrates of stubbles

Defoliation strongly affected the content of water soluble carbohydrates (WSC) of stubbles in both grasses and in both years (Fig. 30). In 1994, the WSC content dropped sharply after defoliation, reached a minimum after approximately eleven days and then increased again. The initial decrease in the WSC content of *D. glomerata* was faster than in *F. pratensis* (species x date interaction significant for days 0 to 5) leading to a higher overall decrease until day 11. After day 11, the WSC content recovered again at a higher rate in *D. glomerata* than in
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*F. pratensis*, leading to a 180% higher WSC content at the second defoliation and even a 203% higher WSC content at the third defoliation.

![Water soluble carbohydrate (WSC) content of stubbles of *Festuca pratensis* (–) and *Dactylis glomerata* (–) in intraspecific shoot competition during regrowth after the first defoliation in 1994 and 1995 as well as after overwintering in spring 1995. ↓ indicates the date of the first, second, and third defoliation. Mean values and standard errors (I) are shown.](image)

Figure 30: Water soluble carbohydrate (WSC) content of stubbles of *Festuca pratensis* (–) and *Dactylis glomerata* (–) in intraspecific shoot competition during regrowth after the first defoliation in 1994 and 1995 as well as after overwintering in spring 1995. ↓ indicates the date of the first, second, and third defoliation. Mean values and standard errors (I) are shown.

As in 1994, the WSC content of stubbles at the first defoliation on 17 May 1995 was higher in *D. glomerata* than in *F. pratensis*, and the initial WSC decrease during the first two weeks of the second regrowth was slightly higher. In contrast to 1994, the WSC content of *D. glomerata* remained at a low level for another week, while the WSC content of *F. pratensis* started to recover during the third week of the second regrowth. In consequence, the recovery of stubble WSC in
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*F. pratensis* swards was considerably faster towards the end of the regrowth period. At the second defoliation, *F. pratensis* surpassed its initial WSC content by 23 %, while the WSC content of *D. glomerata* was 43 % lower.

4.1.9 Root activity in the 0 to 0.12 m soil layer

The root dry weights in the 0 to 0.12 m soil layer of the *F. pratensis* and *D. glomerata* swards at the first defoliation were comparable in both years (Fig. 31). In 1994, regrowth of both species after defoliation was followed by decreasing root dry weights. Relative to *D. glomerata*, the root dry weight of *F. pratensis* at depths of 0 to 0.12 m decreased faster, inducing significantly lower root weights after about one week of second regrowth (Fig. 31A).

In 1995, the root dry weight in *F. pratensis* swards at depths of 0 to 0.12 m was higher than in *D. glomerata* swards at the second defoliation due to a greater increase in root weight during the second half of regrowth (Fig. 31B).

The Rb uptake of *F. pratensis* during the first four to five days of the second regrowth was 52 % (1994) and 41 % (1995) lower as compared to *D. glomerata* (Figs 31C & D). After this initial period, the Rb increase in the shoots of the two grasses was almost similar in both years. The higher Rb uptake of *D. glomerata* at the start of regrowth in 1994 and 1995 was related to a higher SAR for Rb during the first four to five days after defoliation (Figs 31E & F).
Figure 31: Ln-transformed root dry weight in the soil layer from 0 to 0.12 m (A & B), Rubidium (Rb) uptake from 0.06 m below-ground (C & D), and specific absorption rate for Rb (E & F) of Festuca pratensis (▼, ■) and Dactylis glomerata (●, □) in intraspecific shoot competition during regrowth after the first defoliation on 20 May 1994 and 17 May 1995. Each point is the mean of four replicates. A polynomial was fitted through the original data points in (A,B,C & D). I represents the standard errors for the fitted values in (A,B,C & D) and the standard errors of the means in (E & F).
4.2 Analysis of regrowth during the vegetative phase

4.2.1 Residual plant parts

After the third defoliation, the remaining proportion of total plant dry weight in *F. pratensis* swards was significant lower than in *D. glomerata* swards in 1994 and 1995 (Table 7). The residual leaf area in *F. pratensis* swards was considerably higher in both years. In 1994, the stubble dry weight per plant in *F. pratensis* swards was 26% lower than in *D. glomerata* swards but 25% higher in 1995. Compared to *D. glomerata*, the WSC content in stubbles of *F. pratensis* plants was 50% lower in 1994 but 71% higher in 1995. In contrast, root dry weight per plant of *F. pratensis* and the WSC content of roots were significantly higher in both years.

Table 7: The remaining proportion of total plant dry weight, dry weight of stubbles and roots, residual leaf area, and the content of water soluble carbohydrates (WSC) of stubbles and roots, per plant of *Festuca pratensis* and *Dactylis glomerata* in intraspecific shoot competition at the third defoliation on 21 July 1994 and on 20 July 1995. Mean values and standard errors (s.e.) are shown.

<table>
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<th>Parameters</th>
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<th><em>D. glomerata</em></th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>Remaining proportion of total plant dry weight (%)</td>
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</tr>
<tr>
<td></td>
<td>1995</td>
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<td>69.0</td>
<td>1.7</td>
</tr>
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<td>1994</td>
<td>1110</td>
<td>869</td>
<td>52.0</td>
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<td>1995</td>
<td>1113</td>
<td>556</td>
<td>59.9</td>
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<tr>
<td>Residual leaf area (cm² plant⁻¹)</td>
<td>1994</td>
<td>5.5</td>
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</tr>
<tr>
<td></td>
<td>1995</td>
<td>11.9</td>
<td>1.5</td>
<td>0.8</td>
</tr>
<tr>
<td>WSC content of stubbles (mg plant⁻¹)</td>
<td>1994</td>
<td>101</td>
<td>203</td>
<td>20.1</td>
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<tr>
<td></td>
<td>1995</td>
<td>130</td>
<td>76</td>
<td>12.6</td>
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<tr>
<td>WSC content of roots (mg plant⁻¹)</td>
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<td>103</td>
<td>55</td>
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<td>1995</td>
<td>52</td>
<td>6</td>
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</table>
4.2.2 Analysis of regrowth after defoliation in mid-July

Ln-transformed total dry weight of both grasses increased linearly during regrowth after the defoliation on 21 July 1994 (Fig. 32A). RGR of *F. pratensis* based on total dry weight was, on average, slightly lower (0.075 mg mg$^{-2}$ day$^{-1}$) than RGR of *D. glomerata* (Fig. 32B). As during the second regrowth, *D. glomerata* reached a consistently higher LAR approximately one week after defoliation (Fig. 32C). These differences in LAR were mostly caused by a 32% lower SLA of *F. pratensis* as compared to *D. glomerata* and to a much lesser extent by a lower LWR (Figs 32E & F).

In contrast to 1994, the remaining total dry weight of *F. pratensis* after defoliation in July 1995 was considerably higher relative to *D. glomerata* (Fig. 33A). Similar to the second regrowth in both years, regrowth after defoliation was characterised by an initial period of dry weight loss. RGR of *D. glomerata*, based on total dry weight, was slightly higher than that of *F. pratensis* during the first two weeks of regrowth (Fig. 33B). This initial advantage of *D. glomerata* was attributed to a higher NAR (Fig. 33D). LAR increased at a similar rate during the first half of regrowth (Fig. 33C), since *F. pratensis* compensated its lower SLA by a consistent higher LWR (Figs 33E & F). As in 1994, LAR became significantly lower for *F. pratensis* than for *D. glomerata* towards the end of regrowth, mainly due to differences in SLA.
Figure 32: Ln-transformed dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), and leaf weight ratio (F) of Festuca pratensis (▼,●●) and Dactylis glomerata (●,——) in intraspecific shoot competition during a vegetative regrowth after the third defoliation on 21 July 1994. Each point is the mean of four replicates. A first-order polynomial was fitted through the Ln-transformed original dry weights in graph (A). I represents the standard errors for the fitted values in (A, B & D) and standard errors of the means in (C, E & F).
Figure 33: Ln-transformed dry weight (A), relative growth rate (B), leaf area ratio (C), net assimilation rate (D), specific leaf area (E), and leaf weight ratio (F) of Festuca pratensis (▼,••••) and Dactylis glomerata (●,—) in intraspecific shoot competition during a vegetative regrowth after the third defoliation on 20 July 1995. Each point is the mean of four replicates. A second-order polynomial was fitted through the Ln-transformed original dry weights in (A). I represents the standard errors for the fitted values in (A, B & D) and the standard errors of the means in (C, E & F).
4.1.3 Changes in leaf attributes during regrowth

The relative growth rate of leaf area in *F. pratensis* swards was significantly lower during the first two weeks of regrowth in July 1994 (Fig. 34B). The lower RGRLA reduced the advantage of the greater remaining leaf area and caused a consistently lower leaf area of *F. pratensis* two weeks after defoliation (Fig. 34A). The lower leaf area of *F. pratensis* during the second half of regrowth was related to its relatively small leaves, while leaf number was similar to that of *D. glomerata* over this period (Figs 34C & D). The smaller leaf size of *F. pratensis* was the combined result of shorter and narrower leaves (Figs 34E & F).

The principal species-specific differences in the change in leaf attributes during regrowth after the harvest of 20 July 1995 were similar to the corresponding regrowth period in 1994 (Fig. 35). In contrast to 1994, a large part of the increasing differences in average leaf size during regrowth (Fig. 35C) was compensated by a higher leaf number of *F. pratensis* (Fig. 35D). Nevertheless, the total leaf area per plant of *F. pratensis* was 22% lower at the end of regrowth (Fig. 35A).
Figure 34: Ln-transformed leaf area (A), relative growth rate of leaf area (RGRLA) (B), average leaf size (C), leaf number per plant (D), average leaf length (E), and average leaf width (F) of Festuca pratensis (▼,••••) and Dactylis glomerata (●,—) in intraspecific shoot competition during regrowth after the third defoliation on 21 July 1994. Each point is the mean of four replicates. A third-order polynomial was fitted through the original leaf area data points in (A). I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).
Figure 35: Ln-transformed leaf area (A), relative growth rate of leaf area (RGRLA) (B), average leaf size (C), leaf number per plant (D), average leaf length (E), and average leaf width (F) of Festuca pratensis (▼, ◆—) and Dactylis glomerata (●, —) in intraspecific shoot competition during regrowth after the third defoliation on 20 July 1995. Each point is the mean of four replicates. A second- and a third order polynomial was used to fit the original leaf area data points in (A). 1 represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).

III Plant architecture, biomass allocation and regrowth
4.2.4 Changes in canopy structure during regrowth

Differences in leaf attributes influenced the leaf area density distribution in different canopy layers of *F. pratensis* (Figs 36A & C) and *D. glomerata* swards (Figs 36B & D) in intraspecific shoot competition during regrowth after the third defoliation in 1994 and 1995.

Figure 36: Changes in the vertical distribution of leaf area density of *Festuca pratensis* (A & C) and *Dactylis glomerata* (B & D) in intraspecific shoot competition during a vegetative regrowth after the third defoliation on 21 July 1994 and 20 July 1995, respectively. The bars represent the cumulative vertical distribution of leaf area density 5(6) days, 11(13) days, 19(20) days, and 28(33) days after defoliation in 1994 and 1995. Mean values and standard errors (I) are shown.

After the first week of regrowth after 21 July 1994, *D. glomerata* began to place its leaf area preferentially into the upper strata of the canopy. In *F. pratensis* swards, however, a large proportion of the newly produced leaf area was found in
the strata between 0.05 and 0.15 m (Figs 36A & B). At the end of regrowth, the leaf area of *D. glomerata* was greater than that of *F. pratensis* by 59 %, having a 35-fold leaf area density in the uppermost canopy strata and a 2.7-fold leaf area density in the strata between 0.15 and 0.23 m.

In 1995, canopy height of *F. pratensis* was approximately the same as *D. glomerata*, and leaf area density was higher, during the first two weeks of regrowth (Figs 36C & D). Thereafter, the species-specific change in leaf area distribution was the same as during the corresponding regrowth period in 1994. In *F. pratensis* swards only 51% of the foliage produced between day 20 and 33 of regrowth was found in the strata above 0.15 m as compared to 66 % in *D. glomerata* swards.

### 4.2.5 Water soluble carbohydrates of stubbles

Averaged over the whole regrowth period, the WSC content in stubbles of *F. pratensis* was 44 % lower in 1994 but similar to *D. glomerata* in 1995 (Fig. 37). In contrast to *D. glomerata*, the WSC content in stubbles of *F. pratensis* was almost unaffected by regrowth in 1994.

![Graph showing WSC content in stubbles of *Festuca pratensis* and *Dactylis glomerata*](image)

**Figure 37:** Water soluble carbohydrate (WSC) content of stubbles of *Festuca pratensis* (▼,•••) and *Dactylis glomerata* (●,—) grown in intraspecific shoot competition during regrowth after the third defoliation on 21 July 1994 and 20 July 1995, respectively. Mean values and standard errors (I) are shown.
4.2.6 Biomass allocation to shoots and roots

The biomass allocation to the roots was consistently higher for *F. pratensis* than for *D. glomerata* during the whole regrowth period after the defoliation in July in both years (Fig. 38). The Ln-shoot to Ln-root ratio of *F. pratensis* at the start of the regrowth period was 7.9 % lower than that of *D. glomerata* in 1994 and 7.6 % lower in 1995. Differences between the two species increased to 8.5 % at the end of regrowth in 1994 and to 10.3 % in 1995.

![Figure 38: Biomass allocation to shoot and roots of Festuca pratensis (▼,●●●●) and Dactylis glomerata (●,—) grown in intraspecific shoot competition as a function of days after the third defoliation on 21 July 1994 and 20 July 1995 respectively. Mean values of the Ln-shoot to Ln-root ratio and standard errors (I) are shown.](image)

4.2.7 Root activity in different soil layers

The root dry weight of *F. pratensis* at soil depths of 0 to 0.12 m and 0.24 to 0.36 m was generally higher than that of *D. glomerata* over the whole regrowth period from mid-July to mid-August in both years (Figs 39 & 40).
Figure 39: Ln-transformed root dry weight in the soil layer from 0 to 0.12 m (A & B), Rubidium (Rb) uptake at 0.06 m below-ground (C & D), and specific absorption rate for Rb (E & F) of *Festuca pratensis* (▼, ■) and *Dactylis glomerata* (●, □) in intraspecific shoot competition during regrowth after the third defoliation on 21 July 1994 and 20 July 1995. Each point is the mean of four replicates. Second-order polynomials were fitted through the Ln-transformed root dry weights in (A & B). I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).
In 1994, the root weight of both grasses in the soil layer of 0 to 0.12 m decreased after defoliation, reached a minimum and increased again to initial values at the end of regrowth (Fig. 39A). In 1995, differences in root weight of *F. pratensis* and *D. glomerata* from 0 to 0.12 m were greater than in 1994 (Fig. 39B). In contrast to 1994, the decrease in root dry weight of both species lasted for the whole regrowth period.

Despite the 21 % higher average root weight, *F. pratensis* absorbed 15 % less rubidium during the first five days of regrowth in 1994 due to a 61 % lower specific absorption rate for Rb (SAR-Rb) in this period (Figs 39A, C & E). Averaged over the first 13 days of regrowth, differences in SAR in the soil layer from 0 to 0.12 m were also consistent in 1995 (Fig. 39F).

In the soil layer of 0.24 to 0.36 m, the root dry weight of *F. pratensis* was, on average, 69 % lower that of *D. glomerata* 76 % lower as opposed to at 0 to 0.12 m and not affected by regrowth in 1994 (Fig. 40A). As in the upper soil layer, differences in root weight between *F. pratensis* and *D. glomerata* were higher in 1995 (Fig. 40B).

Similar to the Rb uptake from 0 to 0.12 m, the lithium uptake was used to estimate SAR in the soil layer from 0.24 to 0.36 m. In agreement with the results of Rb uptake, the Li uptake of *F. pratensis* after defoliation was consistently slower relative to *D. glomerata* in both years (Figs 40C & D). SAR- Li of both species was in the same range as SAR-Rb in both years (Figs 40E & F). As in the upper soil layer, SAR-Li was high at the beginning of regrowth and decreased thereafter. SAR-Li of *F. pratensis* was again considerably lower than that of *D. glomerata* at the start of regrowth in both years.
Figure 40: Ln-transformed root dry weight in the soil layer from 0.24 to 0.36 m (A & B), Lithium (Li) uptake from 0.30 m below-ground (C & D), and specific absorption rate for Li (E & F) of *Festuca pratensis* (▼, ■) and *Dactylis glomerata* (●, □) in intraspecific shoot competition during regrowth after the third defoliation on 21 July 1994 and 20 July 1995. Each point is the mean of four replicates. A first-order polynomial was fitted through Ln-transformed original root dry weights in (A & B). I represents the standard errors for the fitted values in (A & B) and the standard errors of the means in (C, D, E & F).
Differences in SAR at soil depths of 0 to 0.12 m and 0.24 to 0.36 m were consistent for the phosphorus and potassium uptake averaged over the first five days of regrowth at the end of July 1994 (Figs 41A & C). In 1995, the average SAR of phosphorus and potassium in both species was very low during the first 12 days of regrowth but increased strongly during the following eight days (Figs 41B & D). Compared to D. glomerata, the SAR-K of in F. pratensis was 92 % lower and the SAR-P was 68 % lower between day 12 and day 20 of regrowth.

Figure 41: Specific absorption rate (SAR) for potassium (A & B) and phosphorus (C & D) of Festuca pratensis (■) and Dactylis glomerata (□) in intraspecific shoot competition during regrowth after the third defoliation on 21 July 1994 and 20 July 1995. The bars represent the average SAR calculated for the time period from 0 to 6, 6 to 11, 11 to 19, and 19 to 28 days after defoliation in 1994 and the average SAR from 0 to 12, 12 to 20, and 20 to 33 days after defoliation in 1995. Each bar is the mean of four replicates. I indicates the standard errors of the means.
5. DISCUSSION

At high soil fertility, a rapid replacement of photosynthetic tissue after defoliation or a high adaptive potential of leaf attributes to changing environmental conditions can be important for competitive success (Grime 1979). Species often differ in their ability to promote regrowth, to re-establish foliage and to convert carbon and nutrients into new photosynthetic tissue and other plant structures. We hypothesised that an inherently low regrowth capacity during vegetative growth might be responsible for the decreasing shoot competitive ability of *F. pratensis* during summer. This is supported by growth chamber experiments, in which *F. pratensis* displayed a lower regrowth capacity than *D. glomerata* due to slower refoliation after defoliation (Fig. 3, page 33). The present field study has clearly shown that, based on RGR, there are only slight differences in regrowth capacity as long as regrowth is not hampered by differences in the proportion of remaining shoot meristems. Depending on season and year, there seem to be two groups of factors limiting the competitive ability of *F. pratensis*: (i) a lower regrowth capacity due to a lower proportion of vegetative tillers after the reproductive growth cycle and (ii) differences in leaf attributes and in the pattern of allocation to shoots and roots.

5.1 High growth capacity of *F. pratensis* during the reproductive growth cycle

Although *F. pratensis* is generally known to be a weaker competitor than *D. glomerata*, its competitive ability and yield in binary mixtures during the reproductive growth cycle is relatively high (Gügler 1993; Carlen 1994; Malinowski 1995). The similar shoot yield of *F. pratensis* and *D. glomerata* in intraspecific shoot competition at the first defoliation in both years (Table 5) confirms the above findings. The present study showed that several factors are responsible for the relatively high competitive ability of *F. pratensis* during the reproductive growth cycle.
The RGR in intraspecific shoot competition in reproductive swards of *F. pratensis* was considerably higher than in *D. glomerata* swards (Fig. 23B). The faster increase in LAR, and the higher NAR of *F. pratensis* (Figs 23C & D), which equally explained the higher RGR until the end of April, were probably related to an earlier start of growth processes in spring or to a higher growth activity at low temperatures. This assumption is supported by the substantially lower stubble WSC content of *F. pratensis* already in early April (Table 4) as well as the higher LWR and RGRLA until mid-April (Figs 23F & H). The higher growth could be explained by a lower optimum growth temperature of *F. pratensis* relative to *D. glomerata* and other grasses (Jelmini & Nösberger 1978; Buhring 1990; Carlen 1994).

After mid-April, the changes in canopy architecture of both species were similar and the total leaf area (Fig. 23G) and vertical leaf area distribution (Fig. 24) were comparable. There was no indication that stem elongation did not begin at the same time, since stem dry weight in the different canopy layers of both species increased equally (data not shown). Hence, the similar changes in canopy structure of both species were probably the result of the equal proportion of reproductive tillers, and the approximately similar begin and amount of stem elongation.

The NAR of *F. pratensis* during the reproductive growth cycle was generally higher than that of *D. glomerata*. These findings confirm results of growth chamber experiments with vegetative plants (Fig. 1, page 30). In May, differences in NAR became more important than differences in LAR for the higher RGR of *F. pratensis*. Differences in leaf attributes due to the low SLA are the most important parameter for the relatively high NAR of *F. pratensis* during the vegetative phase (Bühring 1990). During reproductive growth, however, the higher transmission of PPFD in *F. pratensis* swards (Fig. 24) was presumably more important for explaining the higher NAR, since a higher proportion of leaves could be placed in canopy layers with more favourable light conditions.

In 1994, the proportion of reproductive tillers of *F. pratensis* (75 %) was extremely high when compared to *D. glomerata* (52 %). These findings are in line with studies by Gügler (1993) and Carlen (1994). In 1995, the proportion of
reproductive tillers was only 26 % and similar for both species. This was probably a result of the large number of tillers produced in late autumn in 1994 and early spring in 1995 many of which did not reach the critical stage for being vernalized (Table 4). This is supported by comparing the absolute number of reproductive tillers, which was only slightly different in both years (Table 5).

Due to its high proportion of reproductive tillers in 1994, *F. pratensis* reached a higher relative leaf area density in the uppermost canopy layer than *D. glomerata* in interspecific shoot competition (Fig. 18, page 69). Hence, depending on the year, the relatively high proportion of reproductive tillers may be an additional important determinant for shoot competitive ability of *F. pratensis* during the reproductive growth cycle.

### 5.2 Contrasting regrowth capacity after the reproductive growth cycle

#### 5.2.1 Low proportion of remaining shoot meristems

Regrowth in grasses is dependent on three types of meristems. It is most rapid from apical or intercalary meristems at the base of existing tillers, intermediate from the activity of leaf primordial meristems and slowest from the stimulation of axillary buds (Briske 1986). After initiation of stem elongation in a reproductive sward, the apical meristem and some of the axillary buds of reproductive tillers are carried above the level at which defoliation takes place. Once the apex has been removed the tiller dies; regrowth thus depends on the number and developmental status of the remaining undecapitated tillers (Davies 1988). If no active shoot meristems remain after defoliation, re-establishment of leaf area depends on the activation of axillary buds and the production of new tillers and is therefore relatively slow (Caldwell 1981).

In *F. pratensis*, the apex was removed from 75 % of the tillers at the first defoliation in 1994. Conversely, only 52 % of the tillers of *D. glomerata* lost all their shoot meristems (Table 5). The lower proportion of remaining shoot meristems dramatically reduced the regrowth capacity of *F. pratensis* (Fig. 25). In contrast, in 1995 when the proportion of active shoot meristems was similar in
both species, no species specific differences in regrowth capacity were observed (Fig. 26). Consequently, the proportion of active shoot meristems remaining after defoliation had an overriding impact in contributing to a rapid regrowth after the reproductive growth cycle. This supports the general view that, after the reproductive growth cycle, the most important factor for a rapid regrowth is the presence of remaining active shoot meristems after defoliation (Richards & Caldwell 1985; Davies 1988; Richards 1993).

In 1994, the remaining proportion of total dry weight after the first defoliation of *F. pratensis* was clearly lower than for *D. glomerata* (Table 6). Regrowth of both species was followed by an initial period of dry weight loss and an increase in total dry weight at the end of regrowth (Fig. 25A). This period of dry weight loss after defoliation together with a negative RGR lasted about 18 days for *F. pratensis* but only about 10 days for *D. glomerata*. As a result, species-specific differences in total dry weight increased dramatically until the end of regrowth. There were several parameters contributing to the longer period of dry weight loss and slower growth of *F. pratensis* which, apparently, were related to the higher proportion of shoot meristems removed by defoliation. One important parameter was probably the slower resynthesis during the first two weeks of regrowth (Fig. 27A), leading to a longer period of negative carbon balance relative to *D. glomerata*. The slower resynthesis of *F. pratensis* was the result of its lower total dry weight (similar increase in LAR; Fig. 25C) and a smaller increase in leaf size (Fig. 27C), caused by a lower leaf width (Fig. 27F). Conversely, *F. pratensis* re-established its leaf area faster than *D. glomerata* in 1995 (Fig. 28A), due to a faster increase in LAR (Fig. 26C) caused by a higher leaf number (Fig. 28D). Hence, *F. pratensis* probably needs a higher leaf number to build up a leaf area similar to that of *D. glomerata* in order to compensate for its narrower leaves.

### 5.2.2 Contrasting carbohydrate availability

The difference between assimilate use and assimilate production in temperate grasses is in general stored as carbohydrates in stubbles (Davies 1988). Though current photosynthesis of residual leaf area is often a major carbon source for
regrowth after defoliation (Caldwell et al. 1981; Richards & Caldwell 1985; De Visser, Vianden & Schnyder 1997), stored carbohydrates may limit initial regrowth if all leaf area is removed by defoliation (Davies 1988; Richards 1993). There was no residual leaf area after the first defoliation in 1994 (Table 6). Furthermore, the rapid decrease in WSC contents after defoliation indicated a high demand for carbohydrates relative to the supply from current photosynthesis (Fig. 30). The WSC content in stubbles of \textit{F. pratensis} was only 47 mg as compared to 105 mg in stubbles of \textit{D. glomerata} (Table 6). Thus, the lower initial increase in the average leaf size of \textit{F. pratensis} in 1994 might have been related to the lower availability of C due to its depleted WSC content. Indeed, there was a slower and absolutely lower initial mobilisation of WSC in \textit{F. pratensis} than in \textit{D. glomerata}. A lower availability of C for leaf growth might also have been a direct consequence of the lower proportion of active shoot meristems, since some of the WSC reserves were possibly used by other respiring sinks while activating axillary buds (Richards & Caldwell 1985; Richards 1993). This is supported by the initially smaller increases in the leaf number of \textit{F. pratensis} than in \textit{D. glomerata} (Fig. 27D).

Increasing carbohydrate contents after defoliation indicate that C assimilation exceeds the immediate demands of the plant. Hence, the lower WSC restoration in \textit{F. pratensis} during the second regrowth (Fig. 30) and the dramatically lower WSC content until mid-August (Fig. 37) support the conclusion of a relatively low availability of C. In contrast, in 1995 when the proportion of reproductive tillers was similar, the WSC restoration in \textit{F. pratensis} was faster or similar to that in \textit{D. glomerata} (Figs 30 & 37). This underlines the paramount significance of the proportion of remaining active shoot meristems for C availability after defoliation.

\subsection*{5.2.3 Decreasing root weight of \textit{F. pratensis} plants}

The root dry weight of both species in soil layers from 0 to 0.12 m at the first defoliation was comparable in both years (Fig. 31). Regrowth was followed by a decreasing root dry weight in both species and years. In 1994, the decline in root dry weight after defoliation of \textit{F. pratensis} was much higher than for
D. glomerata (Fig. 31A). A similar response was found in the deeper soil layers, though differences were less pronounced and not significant (data not shown). This greater decline in root dry weight was another important parameter contributing to the longer period of dry weight loss in F. pratensis. Root growth and root maintenance is extremely sensitive to shoot defoliation. Hence, root growth, respiration, and nutrient absorption are greatly inhibited after defoliation in rapidly growing plants (Richards 1993). Root growth of F. pratensis was probably curtailed to a greater extent or for a longer period after defoliation because of a relatively high allocation of resources to the shoots to support refoiiation and tillering. Since decapitated tillers cannot continue to grow, their roots die and begin to decompose soon after defoliation (Davies 1988). Due to its higher proportion of decapitated tillers, it is expected that decomposing roots largely contributed to the decreasing root dry weight of F. pratensis during regrowth. Furthermore, even if the root respiration rate was suppressed, more carbon was probably lost by the death of roots in F. pratensis and by the respiration of roots which died later.

5.2.4 Reduced shoot competitive ability?

The relatively high proportion of reproductive tillers of F. pratensis in combination with the high growth capacity at low temperatures, increased its shoot competitive ability during the reproductive growth cycle in spring. In contrast, the higher proportion of shoot meristems removed by defoliation strongly reduced the regrowth capacity of F. pratensis after the first defoliation. Therefore, depending on the year, the lower regrowth capacity after the reproductive growth cycle will reduce the competitive ability of F. pratensis relative to companion grasses such as D. glomerata. In intensively managed swards, F. pratensis cannot take advantage of its higher proportion of reproductive tillers by a higher potential generative propagation by seed (Zimmermann 1995). Hence, the consequences of a high proportion of reproductive tillers were largely negative. To improve the competitive ability of F. pratensis in intensively managed swards, a major breeding aim should be to select for cultivars with a low proportion of reproductive tillers. However, by
comparing leaf growth and root attributes of both species during vegetative growth our results show that, apparently, there are also other factors which limit the shoot competitive ability of *F. pratensis*.

### 5.3 Leaf development during vegetative growth - the key factor for shoot competitive ability?

RGR, based on total dry weight, was similar for both species in intraspecific shoot competition during regrowth after mid-July in 1994 (Fig. 32B) and in May 1995 (Fig. 26B). During the summer in 1995, RGR of *F. pratensis* was initially slightly lower but comparable to that of *D. glomerata* after two weeks of regrowth (Fig. 33B). Consequently, based on RGR, there were only slight differences in regrowth capacity after defoliation as long as regrowth was not hampered by a different proportion of remaining shoot meristems. From these results, it is postulated that a lower RGR is probably the consequence rather than the cause of the low shoot competitive ability of *F. pratensis* relative to *D. glomerata* in fully vegetative plants. RGR of *F. pratensis* may be reduced towards the end of the regrowth period due to shading by *D. glomerata*. However, RGR of *F. pratensis* may also be reduced at the start of regrowth due to shading during the previous growth period, as is, for example, found in field-grown *Lolium perenne* (Thomas & Davies 1978). Thus, factors other than an inherently low regrowth capacity during vegetative growth might be responsible for the decreasing shoot competitive ability of *F. pratensis* during summer.

#### 5.3.1 Contrasting refoiliation

A rapid refoiliation after defoliation may be important for competitive success (Grime 1979). In the present study, the refoiliation of vegetative plants of *F. pratensis* and *D. glomerata* was characterised by two different phases: an initial phase lasting about one (1994) to two weeks (1995), during which *F. pratensis* compensated for its generally lower SLA by a higher LWR. Hence, LAR of both species increased similarly. A second phase, lasting for the rest of the regrowth period during which *D. glomerata*, the better shoot competitor,
considerably increased its LAR compared to *F. pratensis*. The second phase was clearly more important for shoot competition during the vegetative phase. Initial refoiiation of grasses strongly depends on the quantity and quality of the plant material remaining after defoliation (Davies 1988). In vegetative grass plants, the stubbles left behind after defoliation are composed mainly of fully expanded leaf sheaths, containing expanding and differentiating parts of immature leaves, and the basal part of leaves that escaped defoliation. Under favourable environmental conditions, current photosynthesis of the residual and newly expanded leaf area becomes the predominant carbon source for leaf growth within a few days after defoliation (Caldwell et al. 1981; Richards & Caldwell 1985; De Visser, Vianden & Schnyder 1997). Except for after the first defoliation in 1994, the refoiiation of *F. pratensis* was initially quite fast, independent of the contrasting initial WSC content of the stubbles in 1994 and 1995 (Figs 30 & 37). In both years, this led to a higher total leaf area for about one week of regrowth relative to *D. glomerata*, despite a consistently lower RGRLA (Figs 34 & 35). The higher initial refoiiation of *F. pratensis* was probably explained by its higher residual leaf area in both years (Table 7) and by the higher leaf number in 1995 (Fig. 35D). The higher residual leaf area was caused by the higher proportion of small tillers but also by the large proportion of leaf area near the ground (Fig. 36). The first leaf tissue exposed above the defoliation level consists of cells which were completely differentiated at the time of defoliation. Leaf elongation during this initial phase is due to cell expansion of immature leaves, probably a result mainly of spatial and chemical dilution of biomass (De Visser, Vianden & Schnyder 1997). Independent of the year, average leaf length (Figs 34E & 35E) and canopy height (Fig. 36) of both species increased similarly for the first week of regrowth. Hence, it can be expected that both species have a similar capacity for extension growth during this initial phase of regrowth. In line with these findings, *F. pratensis* showed an even higher leaf elongation right after defoliation in growth chamber experiments, although WSC reserves were extremely low (Fig. 3, page 33). Thus, leaf elongation right after defoliation does not seem to be a limiting factor for shoot competition between *F. pratensis* and *D. glomerata*. 
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After this initial phase, increasing differences in leaf attributes and canopy structure of the two species were observed. *D. glomerata* considerably increased its LAR relative to *F. pratensis* due to its higher SLA (Figs 32 & 33). In addition, *D. glomerata* strongly increased its average leaf length relative to *F. pratensis* (e.g. Fig. 35E) and placed a higher proportion of its leaf area into the upper canopy layers (Fig. 36).

With increasing canopy height during refoiiation, differences in the arrangement of leaves, plant height, and biomass allocation to the shoot become more important for shoot competition (Caldwell 1987; Holt 1995). It is generally accepted that a high LAR is a major determinant of a high RGR and an important advantage in competition for light (Poorter 1989; Lambers & Poorter 1992; Garnier 1992). Despite the striking differences in canopy architecture, no species-specific differences in RGR occurred in intraspecific shoot competition due to a slightly higher NAR of *F. pratensis* towards the end of regrowth (e.g. Fig. 33D). In contrast, the higher LAR of *D. glomerata* was an important advantage in competition for light in interspecific shoot competition during the vegetative phase (Fig. 18, page 69). The higher leaf elongation during the second half of regrowth probably increased the capacity of *D. glomerata* relative to *F. pratensis* to capture resources.

5.3.2 Differences in shoot sink

Increased leaf and stem elongation and biomass allocation to the shoot in grasses were reported to occur in response to changes in light quantity and quality imposed by shading (Jelmini & Nösberger 1978; Allard, Nelson & Pallardy 1991; Olff 1992; Holt 1995). Leaf elongation and the shoot sink in *D. glomerata* probably increased relative to *F. pratensis* because of intensified self-shading during the second half of regrowth. This is supported by the increasing biomass allocation to the shoot towards the end of regrowth (Fig. 38), the higher light interception (Fig. 18, page 69), and the increasing SLA in the lowest canopy strata on 21 June and 22 August 1995 (Fig. 42).

Conversely, a relatively low shoot sink of *F. pratensis* might be explained by the relatively high biomass allocation to the roots, the higher WSC content of roots
Plant architecture, biomass allocation and regrowth during summer (Table 7), and the decreasing SLA in the lower canopy layers (Fig. 42).

Contrary to *D. glomerata*, in response to the changed quantity and quality in interspecific shoot competition, *F. pratensis* accelerated its biomass allocation to harvested plant parts (Fig. 16, page 65). Nevertheless, *F. pratensis* was still shaded by *D. glomerata*. In growth chamber experiments *F. pratensis* showed a lower and slower adaptability of SLA to reduced light conditions than did *D. glomerata* (Fig. 6, page 37). Hence, leaf morphology of *F. pratensis* is probably not as adaptable to changes in environmental conditions as it is in *D. glomerata*.

### 5.4 Contrasting rate of nutrient acquisition

The root activity pattern during regrowth was measured in two soil layers to explain the generally lower resource acquisition rate of *F. pratensis* relative to *D. glomerata* (Figs 21 & 22, page 76). Measurements of root activity have the
advantage over measurements of root dry weight and root distribution that they also reflect other root parameters such as age, composition, and physiological status of roots (Tofinga & Snaydon 1992). After the reproductive growth cycle in both years, the marker uptake was relatively slow (Figs 31C & D). SAR was initially low and increased during regrowth (Figs 31E & F). In contrast, during summer when the plants were fully vegetative in the previous growth cycle and soil temperatures were higher, the marker uptake was much faster (Figs 39C & D). SAR was highest during the first week of refoliation and decreased thereafter, thus coincided with RGRLA (Figs 39E & F).

After defoliation, root growth, root respiration, and nutrient absorption of grasses are inhibited (Richards 1993). After the reproductive growth cycle, the inhibition of resource acquisition was apparently relatively long and strong. In contrast, fully vegetative plants showed no inhibition of resource acquisition or only for a very short period of time. Differences in root mass drastically increased during summer (Figs 39 & 40). There was presumably a trade-off in biomass allocation to above- and below-ground plant parts (Tillman 1988). Nevertheless, independent of soil depth, the marker uptake in *D. glomerata* was consistently faster than in *F. pratensis* due to the higher SAR. These results are confirmed by the higher SAR for potassium and phosphorus (Fig. 41). Hence, the faster refoliating *D. glomerata* had, simultaneously, a higher RGRLA and a higher SAR than *F. pratensis*. Though there was presumably a trade-off in biomass allocation to shoots and roots, there was no apparent trade-off in the ability of *D. glomerata* to explore and acquire above- and below-ground resources, as already suggested by Grime (1979). The greater capacity of *D. glomerata* to acquire nutrients was, however, probably a consequence rather than a cause of the higher RGRLA (Lambers & Poorter 1992). On the contrary, the lower root activity of *F. pratensis* might be a consequence of its lower RGRLA. Since differences in SAR were largest during the first week of regrowth, it might also be related to a longer inhibition of nutrient acquisition after defoliation or be the result of general differences in root morphology and physiology.

Species with a rapid and high resource acquisition can be at an advantage in root competition (Grime 1977; Goldberg 1990). Differences in root activity might be a
determinant of competitive success if water supply is limited. *F. pratensis* is known for its decreasing root competitive ability relative to *D. glomerata* during summer (Carlen 1994). The much lower root activity of *F. pratensis* during the first half of regrowth might be the pivotal trait responsible for this decline in root competitive ability.

### 5.5 Conclusions

*F. pratensis* had a higher RGR during the reproductive growth cycle than *D. glomerata* due to a faster increase in LAR in April and a higher NAR. These parameters, in addition to a higher proportion of reproductive tillers (in 1994), probably explain the relatively high competitive ability of *F. pratensis* during reproductive growth.

In 1994, the lower proportion of vegetative tillers and remaining shoot meristems after the reproductive growth cycle, strongly reduced the regrowth capacity of *F. pratensis* relative to *D. glomerata*. In contrast, during summer when the plants were fully vegetative in the previous growth cycle, the striking differences in canopy architecture and biomass allocation were evidently more important for shoot competitive ability than inherent differences in RGR. A higher RGR, and a higher LAR, caused by a higher SLA, as well as the greater capacity to acquire nutrients might put *D. glomerata* at a clear competitive advantage for both above- and below-ground resources.

Depending on the season and year there seem to be two main groups of factors limiting the competitive ability of *F. pratensis*: (i) a lower regrowth capacity due to a lower proportion of vegetative tillers after the reproductive growth cycle and (ii) a lower average leaf length due to differences in leaf attributes.
IV Regrowth in interspecific shoot competition

PART IV

REGROWTH OF FESTUCA PRATENSIS AND DACTYLIS GLOMERATA AFTER DEFOLIATION - CONSEQUENCES OF INTERSPECIFIC SHOOT COMPETITION

1. SUMMARY

The response of pasture plants to shoot competition may change with season due, for example, to changing species-specific differences in plant architecture and regrowth after defoliation. The whole plant response to interspecific shoot competition and the consequences for regrowth were investigated in the field for Festuca pratensis Huds. (Meadow fescue), a weak shoot competitor, and Dactylis glomerata (Orchard grass) for two years.

The shoot competitive ability of F. pratensis decreased progressively from April to the end of August in both growing seasons. This was a consequence of shading by D. glomerata towards the end of regrowth due to the smaller and shorter leaves of F. pratensis and a generally lower total leaf area per plant. Differences in leaf size increased strongly after three weeks of regrowth. In intraspecific shoot competition F. pratensis reached an average leaf size of 4.2 cm² in contrast to D. glomerata with an average leaf size of 10.8 cm². In response to interspecific shoot competition, F. pratensis increased its average leaf size (+25 %), leaf length (+16 %), and LAR. In contrast, the average leaf size (-25 %), leaf length (-27 %), and LAR of D. glomerata were lower than in intraspecific shoot competition. Despite this contrasting response, D. glomerata reached a considerably higher average leaf size and leaf length than F. pratensis in interspecific shoot competition.

Depending on the season, the shoot competitive ability of F. pratensis was reduced further by a lower regrowth rate after the reproductive growth cycle and reduced shoot growth following defoliation due to previous shading. In response to interspecific shoot competition, F. pratensis increased its shoot growth towards the end of the growth cycle, while neglecting root and stubble
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growth. In contrast, *D. glomerata* increased its root and stubble growth as compared to intraspecific shoot competition. This opposing response led initially to similar competitive ability, based on shoot weight production, but to a fast decreasing competitive ability as expressed by the total dry weight of the plants.

2. INTRODUCTION

Competition for light plays an important role in determining the floristic composition of grasslands. Competition for light occurs among individuals. Its intensity depends on the spatial relations between a plant and its neighbours as well as on the effects of neighbouring plants on resource availability and the ability of a plant to compensate for these effects by means of architectural plasticity and physiology (Tremmel & Bazzaz 1993). The availability of above-ground resources for the different species may change in interspecific shoot competition compared to intraspecific shoot competition. This change in the quantity and spectral quality of light in interspecific shoot competition affects plant growth, morphology, and biomass allocation of the whole plant (Givnish 1988) which, in turn, affects competition for light as well as for nutrients and water (Caldwell 1987; Holt 1995). Hence, to understand the competition process, it is necessary to assess the effects of competition on resource availability of competing species and the response of above-ground and below-ground plant traits to these effects (Goldberg 1990).

The ability of a plant to compete for light may change with season due, for example, to differences in the species-specific responses of plant architecture and regrowth after defoliation to changes in environment. In a dense canopy, the foliage of different species may differ slightly in height, inclination, or orientation and may overlap considerably too. Because of the rapid decline of PAR in dense canopies (Saeki 1963), advantages in competition for light can occur quickly if one species is able to overtop another during regrowth after defoliation (Caldwell 1987; Barnes et al. 1990; Holt 1995). Hence, shoot competition is not only affected by season, but also changes considerably during a growth cycle following defoliation. However, only a small number of field
experiments on shoot competition among regularly defoliated pasture plants lasted long enough to study the seasonal effects of shoot competition (Remison & Snaydon 1980; Martin & Field 1984; Carlen 1994). None of these experiments focused on the whole plant response to shoot competition and the seasonal effects of shoot competition on regrowth after defoliation.

In cooler regions, *Festuca pratensis* Huds. (Meadow fescue) is an excellent herbage grass of high forage quality; it is winterhardy and adapts to humid conditions. It is, however, a weak competitor against companion grasses such as *D. glomerata* and has nearly disappeared from intensively managed grassland on fertile soils during recent decades (Mott 1982; Gügler 1993; Carlen 1994). The lower competitive ability of *F. pratensis* is attributed to a low shoot competitive ability in summer during vegetative growth as a result of a lower leaf area in the upper canopy layers (Fig. 18; page 69). This characteristic may be a consequence of (i) a reduced regrowth capacity after the reproductive growth cycle, (ii) inherent differences in leaf attributes and biomass allocation to shoots and roots, and (iii) a low plasticity of leaf attributes for morphogenetic adaptation in response to interspecific shoot competition.

*F. pratensis* and *D. glomerata* were used to analyse the whole plant response during regrowth to interspecific shoot competition and its effects on subsequent regrowth in an intensively defoliated sward. Specific objectives of the experiment were (1) to compare the regrowth rate in interspecific shoot competition in different seasons under field conditions, (2) to assess the effects of interspecific shoot competition on regrowth after defoliation, (3) to assess the changes in canopy structure during regrowth, and (4) to estimate the response of leaf attributes, biomass allocation in the whole plant, reserve accumulation, and root growth to shoot interspecific competition during regrowth.

The results demonstrate that experiments on shoot competition of pasture plants should focus on the whole plant response for a better understanding of processes involved in shoot competition.
3. MATERIALS AND METHODS

3.1 Experimental method, treatments, and measurements

A field experiment on shoot competition was carried out at the research station of the Swiss Federal Institute of Technology in Eschikon, near Zurich, Switzerland (550 m above sea level) from October 1993 to October 1995. The experiment was a completely randomised block with four replications (four forcing beds of 10 x 1.45 m). The blocks consisted of two swards (2.56 x 1.38 m) with either Festuca pratensis (Meadow fescue) or Dactylis glomerata (Orchard grass) in intraspecific shoot competition and a sward (4.24 x 1.38 m) with the two species in interspecific shoot competition. The swards were defoliated six times per growing season on 20 May, 21 June, 21 July, 18 August, 15 September, and 18 October 1994 and on 17 May, 21 June, 20 July, 22 August, 18 September, and 19 October 1995 (Table 8). Both species were at the reproductive stage at the first defoliation and fully vegetative at subsequent defoliations in both years.

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Table 8: Dates of fully destructive sequential harvests to assess the seasonal variation in regrowth of *F. pratensis* and *D. glomerata* in intra- and interspecific shoot competition in 1994 and 1995. The swards were grown under field conditions and defoliated six times per growing season (↓). In 1994, vegetative regrowth after the first and the third defoliations were analysed (↓). In 1995, the reproductive growth cycle in spring, its relation to vegetative regrowth after the first defoliation, and vegetative regrowth after the third defoliation were analysed.
Fully destructive sequential harvests were made to determine the effects of shoot competition on regrowth after defoliation. In 1994, vegetative regrowth after the first and third defoliation was analysed. In 1995, we analysed the reproductive growth cycle in spring, its relation to vegetative regrowth after the first defoliation, and vegetative regrowth after the third defoliation. The reproductive growth cycle in 1995 was analysed, with sequential harvests on 3 April, 18 April, 1 May, 9 May, and 17 May. Regrowth during the vegetative phase was analysed, with sequential harvests on the day of defoliation (0) and after five to six days, 11 to 13 days, 19 to 21 days, and 28 to 35 days of regrowth.

Further details of the experimental method, plant measurements, and statistics are given in Chapter 3 of Part III.

### 3.2 Effects of shoot competition

Resource complementarity (Snaydon & Satorre 1989) i.e. the extent to which two species share common limited resources, was determined according to the relative yield total (RYT) (de Wit, 1960). RYT, based on total dry weight, did not differ significantly from 1.0. Thus, the two species showed no resource complementarity, indicating that they competed fully for the same limiting resources.

The shoot competitive ability of *F. pratensis* relative to *D. glomerata* was determined by using the competitive balance index (Cbij) based on the total dry weight of the plants (Cbij) (Wilson, 1988). At a RYT of 1.0, variation in Cbij depends on competition effects and can be interpreted as shoot competitive ability. Cbij values were also calculated for shoot yields (Cbijsh), stubble dry weights (Cbjst), and root dry weights (Cbior) in order to estimate the response of different plant parts during regrowth to interspecific shoot competition.
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The Cbij of *F. pratensis*, relative to *D. glomerata* (species j), for a 0.5:0.5 replacement design is:

\[ C_{bij} = \log_e\left(\frac{W_{ij}}{W_{ji}}\right) \left(\frac{W_{ii}}{W_{jj}}\right) \]

Wij and Wji are the total dry weights or the dry weights of the respective plant parts of *F. pratensis* and *D. glomerata* in interspecific shoot competition. Wii and Wjj are the corresponding dry weights when grown in intraspecific shoot competition.

A Cb of zero indicates that both species had the same shoot competitive ability. A positive Cb indicates that *F. pratensis* had a higher shoot competitive ability than *D. glomerata*. A negative Cb indicates that *F. pratensis* was less competitive than *D. glomerata*. Similarly, positive Cb_{sh}, Cb_{st}, and Cb_{sw} values of *F. pratensis* relative to *D. glomerata* indicate a positive response of the respective plant parts to shoot competition. Negative Cb_{sh}, Cb_{st}, and Cb_{sw} values indicate a negative response of the respective plant parts to shoot competition.

Cb, as a measure of shoot competitive ability, is more suitable than, for example, aggressivity (values between 1 and -1) (Mcgilchrist & Trenbath 1971), because the variance of the index is not limited.
4. RESULTS

4.1 Regrowth of *F. pratensis* in shoot competition with *D. glomerata*

Regrowth after defoliation of *F. pratensis* and *D. glomerata* in interspecific shoot competition was typically followed by an initial period of loss in total dry weight followed by an increase in total dry weight (Fig. 43). The total dry weight of *F. pratensis* was generally lower than that of *D. glomerata*, almost independent of season and year.

In 1994, regrowth of *F. pratensis* after the first defoliation was substantially lower than that of *D. glomerata* (Fig. 43A). The consequence was a 16 day period of loss of total dry weight and only a slight increase in total dry weight towards the end the growth cycle. In contrast, *D. glomerata* reached a positive RGR already 10 days after defoliation and showed a substantial increase in total dry weight thereafter (Figs 43A & B). The lower regrowth capacity of *F. pratensis* resulted in a 2% lower total dry weight at the second defoliation than at the beginning of regrowth as compared to a dry weight gain of 27% in *D. glomerata*. At the second defoliation, the total plant dry weight of *F. pratensis* (1232 mg) in interspecific shoot competition was 46% lower than that of *D. glomerata* (2296 mg).

In 1995, both species again experienced an initial period of loss of total dry weight during the second regrowth, lasting for only 14 days for *F. pratensis* but 18 days for *D. glomerata*, followed by an increase in total dry weight (Fig. 43C). In contrast to 1994, RGR of *F. pratensis* was higher than RGR of *D. glomerata* (Fig. 43D). As a consequence, species-specific differences in total dry weight decreased considerably until the end of regrowth.

During the fourth growth cycle in 1994, after the plants had been fully vegetative in the previous growth cycle, Ln-transformed total dry weights of *F. pratensis* increased linearly after defoliation (Fig. 43E). *D. glomerata* accumulated less dry weight for about one week but increased its dry weight considerably as compared to *F. pratensis* during the second half of regrowth.
Figure 43: Regrowth in vegetative swards of *Festuca pratensis* (▼,——) and *Dactylis glomerata* (●,—) in interspecific shoot competition during the second and fourth growth cycles in 1994 and 1995. The course of Ln-transformed total dry weights (A, C, E & G) and the corresponding relative growth rates (B, D, F & H) are shown. Each data point is the mean of four replicates. Original dry weights and fitted curves are shown in the graphs (A, C, E & G). I indicates the standard errors for the fitted values.
During the fourth growth cycle in 1995, the period of dry weight loss after defoliation was again shorter (about 10 days) for both species than during the second regrowth (Fig. 43G). In contrast to 1994, both species showed similar increases dry in weight and RGR in interspecific shoot competition (Fig. 43H).

4.2 Shoot competitive ability and response of shoot, stubble, and root growth

The competitive balance index based on total plant dry weights (Cb) was used to estimate the shoot competitive ability of *F. pratensis* relative to *D. glomerata* (Fig. 44).

In 1994, the shoot competitive ability of *F. pratensis* was similar to *D. glomerata* during the reproductive growth cycle in spring (Cb = 0). After defoliation on 20 May, the shoot competitive ability of *F. pratensis* decreased, mainly during the second (Cb = -0.2) and fourth growth cycles, to a Cb of -0.38 on 18 August. Cbsh of *F. pratensis* relative to *D. glomerata* decreased drastically to -1.2 after five days of the second growth cycle, indicating strong effects of interspecific shoot competition on shoot growth of both species. After this initial decrease, Cbsh rose to zero by the second defoliation. Cb decreased simultaneously, indicating a change in biomass allocation of *F. pratensis* relative to *D. glomerata* in response to interspecific shoot competition.

During the fourth growth cycle in 1994, Cbsh of *F. pratensis* relative to *D. glomerata* dropped initially to -0.8 and then increased, indicating dynamic effects of shoot competition on shoot growth of both species, as during the second regrowth. Cbsh and Cb were significantly lower than Cbsh. Hence, shoot competition affected root and stubble growth of both species more than it did shoot growth.

In 1995, the shoot competitive ability of *F. pratensis* again decreased from the reproductive growth cycle in spring to the fourth defoliation on 22 August. In contrast to 1994, the shoot competitive ability of *F. pratensis* decreased at the end of the reproductive growth cycle (Cb = -0.32) but was similar or slightly higher
Figure 44: Shoot competitive ability of Festuca pratensis relative to Dactylis glomerata, measured by the competitive balance index based on total plant dry weight ($C_b$), during the reproductive growth cycle as well as during the second and fourth, vegetative, growth cycles in 1994 and 1995. The course of $C_b$, based on shoot ($C_{bs}$), stubble ($C_{bs}$), and root dry weight ($C_r$), indicates the response of above- and below-ground plant parts to interspecific shoot competition during regrowth. Means of four replicates and standard errors (I) for the response to shoot competition as well as the mean s.e. for $C_b$ in each year are shown.
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than that of *D. glomerata* during the second regrowth (\(C_{b,2} = -0.23\) at the second defoliation). Thereafter, the shoot competitive ability of *F. pratensis* decreased again, reaching a \(C_{b,3} = -0.61\) by the third defoliation on 20 July.

In contrast to 1994, \(C_{b,sh}\) of *F. pratensis* increased initially during the second regrowth and decreased only slightly to \(-0.18\) at the end of regrowth. In line with the decreasing shoot competitive ability of *F. pratensis* from 21 June to 22 August, effects of shoot competition on different plant parts increased. As in 1994, interspecific shoot competition affected stubble growth (\(C_{bs,2} = -0.76\) on 20 July) and root growth (\(C_{br} = -0.91\)) to a greater extent than shoot growth (\(C_{b,sh} = -0.36\)).

### 4.3 Response of total leaf area to shoot competition

The total leaf area of *F. pratensis* in interspecific shoot competition was lower than that of *D. glomerata* at the end of all analysed growth cycles (Fig. 45).

At the first defoliation in 1994, the total leaf area per plant of *F. pratensis* (204 cm\(^2\)) was 38 % lower than that of *D. glomerata* (331 cm\(^2\)). Vegetative refoliation of *F. pratensis* (84 cm\(^2\)) during the second growth cycle was substantially slower than that of *D. glomerata* (184 cm\(^2\)), leading to a 54 % lower leaf area at the second defoliation on 21 June. Relative leaf area of *F. pratensis* dropped sharply to 0.37, 11 days after defoliation. Hence, its leaf area per plant in interspecific shoot competition (8 cm\(^2\)) was much lower than in intraspecific shoot competition (22 cm\(^2\)). Despite the initially slower refoliation, the total leaf area per plant of *F. pratensis* in intraspecific and interspecific shoot competition was similar at the end of second regrowth. In contrast to *F. pratensis*, refoliation of *D. glomerata* was not affected by shoot competition.

During the fourth growth cycle in 1994, the species-specific differences in total leaf area per plant were less pronounced. At the defoliation on 18 August, leaf area per *F. pratensis* plant (154 cm\(^2\)) was only 29 %, though still significantly lower than that of *D. glomerata* (216 cm\(^2\)). *F. pratensis* increased its leaf area in response to interspecific shoot competition by 13 %. In contrast, leaf area per plant of *D. glomerata* was again not affected by shoot competition.
Figure 45: The response of leaf area development during regrowth to shoot competition in a sward of *Festuca pratensis* and *Dactylis glomerata* in 1994 and 1995. The course of the total leaf area per plant in interspecific shoot competition and the leaf area relative to intraspecific shoot competition during the reproductive growth cycle as well as during the second and fourth, vegetative, growth cycles are shown. I indicates the standard errors.
During the reproductive growth cycle in 1995, the leaf area of both species increased similarly until 1 May. Thereafter, *D. glomerata* increased its leaf area in interspecific shoot competition as compared to *F. pratensis*. As a result, the leaf area of *F. pratensis* was again 25% lower at the first defoliation on 17 May. This smaller increase in leaf area was caused by shoot competition, since the leaf area of *F. pratensis* (273 cm²) and *D. glomerata* (272 cm²) in intraspecific shoot competition was similar.

During the second growth cycle, the species-specific differences in refoiliation were far less pronounced than in 1994. In mixture, both species reached a similar total leaf area for three weeks. At the next defoliation, however, the total leaf area of *F. pratensis* was again 25% lower. Compared to intraspecific shoot competition, refoiliation of both species in mixture was initially reduced but improved towards the end of regrowth. This initial reduction in refoiliation lasted longer in *F. pratensis* (~20 days) than in *D. glomerata* (~11 days).

Species-specific differences in total leaf area per plant on the fourth defoliation in August were consistent with 1994. The total refoiliation of *F. pratensis* in interspecific shoot competition was 22% lower than that of *D. glomerata*. The relative leaf area of *F. pratensis* after the first week of regrowth was 0.77 but no longer differed from one at the next defoliation.

4.4 **Response of leaf attributes to shoot competition**

In both competition treatments the leaves of *F. pratensis* were generally smaller than those of *D. glomerata* at the second and fourth defoliation in both years (Fig. 46).

In intraspecific shoot competition, differences in the average leaf size increased drastically after three weeks of the second growth cycle (Fig. 46A). At the next defoliation after 35 days (1995), *F. pratensis* reached an average leaf size of only 4.2 cm², whereas the average leaf size of *D. glomerata* was 10.8 cm². These substantial species-specific differences in leaf size, were to a large extent, caused by a lower average length of *F. pratensis* leaves (14.5 cm) compared to *D. glomerata* leaves (30.4 cm) (Fig. 46C).
In interspecific shoot competition the average leaf size (+25 %) and average leaf length (+16 %) of *F. pratensis* were higher than in intraspecific shoot competition. In contrast, leaves of *D. glomerata* were, on average, smaller (-25 %) and shorter (-27 %). Nevertheless, *D. glomerata* had larger (+75 %) and longer (+42 %) leaves in interspecific shoot competition than *F. pratensis*.

Figure 46: The response of the average leaf size (A & B) and average leaf length (C & D) to shoot competition in a vegetative sward of *Festuca pratensis* and *Dactylis glomerata* during the second and fourth growth cycles in 1994 and 1995. Means of four replicates in interspecific- and intraspecific shoot competition and second-order regressions over both years are plotted as a function of days after defoliation.
During the growth cycle in August of both years, the main species-specific differences in leaf attributes and their responses to interspecific shoot competition were similar as during the second regrowth (Figs 46B & C). D. glomerata had a smaller average leaf size and shorter leaves than during the second regrowth. Nevertheless, in interspecific shoot competition, its average leaf size (6.5 cm²) was nearly double that of F. pratensis (3.8 cm²) after 33 days of regrowth (1995). LAR of both species was strongly affected by shoot competition (Fig. 47). In intraspecific shoot competition LAR of F. pratensis and D. glomerata increased similarly for one week during the second growth cycle in 1994. Thereafter, LAR of D. glomerata increased strongly to consistently higher values than those of F. pratensis after three weeks of regrowth. In interspecific shoot competition, LAR of F. pratensis was significantly lower than in intraspecific shoot competition during the first two weeks of the second growth cycle but increased to higher values at the end of regrowth. In contrast, D. glomerata did not show such a response to interspecific shoot competition.

In contrast to 1994, F. pratensis reached a higher LAR in 1995 than D. glomerata in intraspecific shoot competition during the first two weeks of the second regrowth. Nevertheless, its LAR at the second defoliation (0.061 cm² mg⁻¹) was again significantly lower than that of D. glomerata (0.075 cm² mg⁻¹). In contrast, in interspecific shoot competition, LAR of both species was similar at the second defoliation due to an increase in LAR of F. pratensis and a decrease in LAR of D. glomerata.

At the end of the growth cycle in August, LAR of F. pratensis in intraspecific shoot competition was lower than that of D. glomerata in 1994 (-31%) and 1995 (-33%). In response to interspecific shoot competition, F. pratensis increased its LAR in 1994 (+35%) and 1995 (+18%). In contrast, D. glomerata reduced its LAR in interspecific shoot competition in 1994 (-14%) and 1995 (-20%). Because of this different response, LAR in interspecific shoot competition was similar for both species at the fourth defoliation in both years.
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Figure 47: The response of the leaf area ratio to shoot competition in a vegetative sward of *Festuca pratensis* and *Dactylis glomerata* during the second and fourth growth cycle in 1994 and 1995. Means of four replicates in interspecific- and intraspecific shoot competition are plotted as a function of days after defoliation. I indicates the standard errors.

4.5 Changes in canopy structure during regrowth in shoot competition

Changes in the distribution of relative leaf area density give an indication of the light interception of both species in interspecific shoot competition during vegetative regrowth in both years (Figs 48 & 50) and during the reproductive growth cycle in 1995 (Fig. 49).
Due to its slow refoiiation, the leaf area density of *F. pratensis* in interspecific shoot competition was low relative to *D. glomerata*, even after only five days of the second regrowth in 1994 (Fig. 48). These large differences in relative leaf area density were consistent throughout the whole growth cycle. In interspecific shoot competition *F. pratensis* reached, on average, a relative leaf area density of only 0.14 after 11 days, 0.17 after 19 days, and 0.33 after 31 days of regrowth. During the fourth growth cycle in 1994, *F. pratensis* reached a higher relative leaf area density in shoot competition with *D. glomerata* after five days of regrowth. Thereafter, the relative leaf area density of *F. pratensis* in the upper canopy layers decreased continuously as a result of its shorter leaves (Fig. 46). At
the next defoliation after 28 days, no leaves of *F. pratensis* were found in the canopy strata between 0.35 and 0.50 m and its relative leaf area density in the strata between 0.23 and 0.35 m was only 0.3.

During the reproductive growth cycle in 1995, the relative leaf area density of *F. pratensis* (0.62) in interspecific shoot competition was slightly higher on 18 April as compared to *D. glomerata* (Fig. 49). During the next two weeks, canopy height increased markedly to 0.35 m, probably due to increasing leaf area and the start of stem elongation. By the harvest of 1 May, *F. pratensis* had reached a higher relative leaf area density (0.76) than *D. glomerata* in the uppermost canopy layer. During May, the relative leaf area density of *F. pratensis* in the uppermost canopy layer decreased to 0.57 (9 May) and 0.47 (17 May). At the first defoliation, the relative leaf area density of *F. pratensis* was lower than that of *D. glomerata* in all canopy layers due to the 25 % lower total leaf area (Fig. 45).

**Figure 49**: Changes in the relative leaf area density in different canopy layers in a reproductive sward of *Festuca pratensis* and *Dactylis glomerata* in interspecific shoot competition during the first growth cycle in 1995. Means of four replicates are shown.

In contrast to 1994, the refoiliation of *F. pratensis* in interspecific shoot competition after the first defoliation in 1995, was faster than that of *D. glomerata* (Fig. 50). Hence, *F. pratensis* reached a higher relative leaf area
density than *D. glomerata* for two weeks of the second regrowth. As in 1994, *D. glomerata* was able to increase its proportion of leaf area in the upper canopy layers during the second half of regrowth. At the end of the growth cycle, the leaf area density of *F. pratensis* was again only 0.07 in the uppermost canopy strata and only 0.30 in the strata between 0.23 and 0.35 m above the soil surface.

![Figure 50](image_url)

**Figure 50:** Changes in the relative leaf area density in different canopy layers in a vegetative sward of *Festuca pratensis* and *Dactylis glomerata* in interspecific shoot competition during the second and fourth growth cycle in 1995. The bars represent the leaf area densities 6, 12 to 13, 20 to 21, and 33 to 35 days after defoliation on 17 May and 20 July. Means of four replicates are shown.

The results of the regrowth period in August were consistent with the growth cycles analysed previously. During the last two weeks of regrowth, *D. glomerata* was again able to place a high proportion of leaves into the upper canopy layers and thus shaded *F. pratensis* with its longer leaves.
4.6 Response of the harvest index to shoot competition

In intraspecific shoot competition, *F. pratensis* reached a lower harvest index than *D. glomerata* during regrowth in August 1994 (0.25 vs. 0.30) and 1995 (0.43 vs. 0.51) (Fig. 51). In interspecific shoot competition, the harvest index of *F. pratensis* increased significantly (by 31% in 1994 and by 33% in 1995), while *D. glomerata* showed a contrasting response (-14% in 1994 and -21% in 1995). Thus, the harvest index of *F. pratensis* reached higher values than that of *D. glomerata* in 1994 (0.33 vs. 0.26) and also in 1995 (0.57 vs. 0.40). Hence, in interspecific shoot competition a higher proportion of plant dry weight was lost by *F. pratensis* than by *D. glomerata* as a result of defoliation.

**Figure 51:** The response of the harvest index to shoot competition in a vegetative sward of *Festuca pratensis* and *Dactylis glomerata* during the fourth growth cycle after defoliation on 21 July 1994 and 20 July 1995. The harvest index stands for the ratio between harvested and remaining plant dry weight. Means of four replicates in interspecific- and intraspecific shoot competition as a function of days after defoliation and standard errors (I) are shown.
4.7 Response of carbohydrate reserves to shoot competition

In interspecific shoot competition, the content of water soluble carbohydrates (WSC) in stubbles of *F. pratensis* was, on average, much lower than in stubbles of *D. glomerata* (Fig. 52). Already at the first defoliation in 1994, the WSC content in *F. pratensis* (35 mg) was significantly lower than that of *D. glomerata* (74 mg). After defoliation, WSC contents decreased to a minimum after about 11 days and then increased again until the second defoliation. The initial decrease in the WSC contents in *F. pratensis* was slower than in *D. glomerata* (species x date interaction significant for day zero to day five), leading to a lower overall decrease until day 11. After day 11, the WSC contents in *F. pratensis* recovered at a lower rate than in *D. glomerata*, again causing a lower WSC content at the second defoliation (25 mg vs. 73 mg). These species-specific differences in WSC contents increased substantially from the second to the third defoliation (61 mg vs. 226 mg).

The relative WSC content in *F. pratensis* decreased to 0.37 at the second and to 0.61 at the third defoliation but did not differ from one in *D. glomerata*. Hence, interspecific shoot competition severely reduced the recovery of WSC reserves in *F. pratensis* as compared to intraspecific shoot competition but did not affect the WSC reserves in *D. glomerata*.

As during the second growth cycle, WSC contents decreased to a minimum after about 11 days and then increased again during regrowth in August. Comparable to the second growth cycle, the absolute and relative decreases in WSC contents in *F. pratensis* during the first 11 days were lower than in *D. glomerata*. Thereafter, the WSC contents in *F. pratensis* again remained at a low level, while those of *D. glomerata* recovered to higher values than before defoliation. As a result, the content (68 mg) and concentration (10.2 %) of WSC in *F. pratensis* in interspecific shoot competition were tremendously lower at the defoliation on 22 August than those of *D. glomerata* (334 mg and 24.3% respectively). Relative to intraspecific shoot competition, the WSC contents in *F. pratensis* were reduced by 33 %, while in *D. glomerata* they increased by 39 %.
Figure 52: The response of the content of water soluble carbohydrates (WSC) in stubbles to shoot competition in a sward of *Festuca pratensis* and *Dactylis glomerata* during regrowth in 1994 and 1995. The WSC contents in interspecific shoot competition and the WSC contents relative to intraspecific shoot competition during the reproductive growth cycle and during the second and fourth, vegetative, growth cycles are shown. I indicates the standard errors.
After overwintering, the WSC contents of *F. pratensis* (133 mg) in interspecific shoot competition were still 55% lower on 4 April 1995 than in *D. glomerata* (292 mg). The WSC contents of both species decreased until 9 May and increased again towards the end of the reproductive growth cycle. The WSC contents at the first defoliation were higher than in 1994, though, as before, lower in *F. pratensis* (97 mg) than in *D. glomerata* (174 mg).

In line with 1994, the WSC contents of *F. pratensis* remained at comparably low levels from the second growth cycle in June to the end of the fourth growth cycle in August. Interspecific shoot competition again led to severely reduced WSC contents in *F. pratensis* and enhanced WSC contents in *D. glomerata*. The effects of shoot competition during the second growth cycle were about the same as in 1994, but increased strongly during the third regrowth period. At the third defoliation, the relative WSC content of *F. pratensis* in interspecific shoot competition was only 0.25 as compared to 2.53 for *D. glomerata*; hence, in intraspecific shoot competition, the WSC content (130 mg) of *F. pratensis* was higher than in *D. glomerata* (76 mg).
4.8 Effects of shoot competition on root growth

The effects of shoot competition on root dry weight were greater than the effects on shoot dry weight (Fig. 44) due to the contrasting species-specific change in biomass allocation (Fig. 51). Figure 53 shows the effects of shoot competition on root dry weight at different soil depths in 1995. Results in 1994 were similar though slightly less pronounced.

![Graph showing the response root growth in different soil layers to shoot competition in a sward of Festuca pratensis and Dactylis glomerata in 1995. The changes in the competitive balance index (Cb), based on root dry weights in soil layers from 0 to 0.12 m, 0.12 to 0.24 m, and 0.24 to 0.36 m of F. pratensis relative to D. glomerata during the reproductive growth cycle and during the second and fourth, vegetative, growth cycles are shown. I indicates the standard errors.](image)

Effects of shoot competition on root dry weight increased strongly from July to the end of August. On 20 July, Cb based on root dry weight at soil depths of 0 to 0.12 m (-0.70) was significantly higher than Cb based on root dry weight at 0.12 to 0.24 m (-1.24) and at 0.24 to 0.36 m (-1.66). Hence, effects of shoot competition on root dry weight increased strongly with increasing soil depth.

The effective root dry weights for of different treatments and soil depths at the defoliation on 20 July 1995 are compared in Table 9.
**IV Regrowth in interspecific shoot competition**

**Table 9:** Dry weight of *Festuca pratensis* and *Dactylis glomerata* roots in different soil depths in interspecific and intraspecific shoot competition after the third defoliation on 20 July 1995. Dry weight of roots from soil depths of 0 to 0.12 m, 0.12 to 0.24 m, and 0.24 to 0.36 m as well as the total dry weights between 0 to 0.36 m are compared. Mean values of four replicates and standard errors (s.e.) are shown.

<table>
<thead>
<tr>
<th>Root dry weight at soil depths of</th>
<th>Shoot competition</th>
<th>Interspecific</th>
<th>Intraspecific</th>
<th>s.e.</th>
</tr>
</thead>
<tbody>
<tr>
<td>(mg plant⁻¹)</td>
<td>(mg plant⁻¹)</td>
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<tr>
<td>0 to 0.12 m</td>
<td><em>F. pratensis</em></td>
<td>417</td>
<td>712</td>
<td>29.0</td>
</tr>
<tr>
<td></td>
<td><em>D. glomerata</em></td>
<td>480</td>
<td>406</td>
<td>30.4</td>
</tr>
<tr>
<td>0.12 to 0.24 m</td>
<td><em>F. pratensis</em></td>
<td>124</td>
<td>286</td>
<td>37.8</td>
</tr>
<tr>
<td></td>
<td><em>D. glomerata</em></td>
<td>166</td>
<td>110</td>
<td>8.0</td>
</tr>
<tr>
<td>0.24 to 0.36 m</td>
<td><em>F. pratensis</em></td>
<td>46</td>
<td>113</td>
<td>26.0</td>
</tr>
<tr>
<td></td>
<td><em>D. glomerata</em></td>
<td>81</td>
<td>38</td>
<td>6.8</td>
</tr>
<tr>
<td>0 to 0.36 m</td>
<td><em>F. pratensis</em></td>
<td>586</td>
<td>1111</td>
<td>78.0</td>
</tr>
<tr>
<td></td>
<td><em>D. glomerata</em></td>
<td>727</td>
<td>554</td>
<td>38.0</td>
</tr>
</tbody>
</table>

The dry weight of *F. pratensis* roots from 0 to 0.12 m was 41 % lower in interspecific shoot competition (417 mg) than in intraspecific shoot competition (712 mg). In contrast, *D. glomerata* reached an 18 % higher root dry weight in interspecific than in intraspecific shoot competition (480 mg vs. 406 mg). With decreasing Cb in higher soil layers, the reduction in root dry weight of *F. pratensis* increased to 59 % (0.24 to 0.36 m), while root dry weight of *D. glomerata* increased to 213 %.

As a result of these strong effects, *F. pratensis* in interspecific shoot competition had a significantly (20 %) lower total root dry weight (586 mg) than *D. glomerata* (727 mg). In contrast, the total root dry weight of *F. pratensis* (1111 mg) in intraspecific shoot competition was double that of *D. glomerata* (554 mg).
5. DISCUSSION

The availability of above-ground resources for plants may be different in interspecific shoot competition than in monoculture. For F. pratensis, the weaker competitor, resource availability decreased with increasing shading in interspecific shoot competition towards the end of regrowth as compared to intraspecific shoot competition. In contrast, the availability of resources of D. glomerata plants increased during regrowth in shoot competition with F. pratensis as compared to intraspecific shoot competition. These contrasting changes in the availability of above-ground resources caused by shoot competition affected the growth of the whole plant. This change was marked by a shift in biomass allocation to shoots and roots as well as by altered leaf growth and reserve accumulation. The contrasting changes in morphology and physiology of both species in turn affected their competitive ability for above-ground but also for below-ground resources.

The most important limitation of the shoot competitive ability of F. pratensis was shading by D. glomerata towards the end of regrowth during the vegetative phase. Depending on the season, the reasons were (i) a limited plasticity of leaf attributes in the response to interspecific shoot competition which did not compensating for differences in SLA, (ii) a reduced regrowth rate after the reproductive growth cycle, and (iii) reduced shoot growth after defoliation due to previous shading in interspecific shoot competition. Results have also shown that processes of shoot competition in pasture plants are better understood when the response of the whole plant is studied. Interpretations of competitive ability based on the shoot response only may be misleading.

The contrasting responses of both species to the changed availability of light in interspecific shoot competition and their consequences for the interpretation of shoot competitive ability will be discussed briefly.
5.1 Limited response of leaf attributes to shoot competition

The shoot competitive ability of *F. pratensis* relative to *D. glomerata* decreased progressively from April to the end of August in both growing seasons (Fig. 44). The decline in shoot competitive ability of *F. pratensis* was a consequence of shading by *D. glomerata* towards the end of regrowth during the vegetative phase. At defoliation, the proportion of leaf area of *F. pratensis* in the upper canopy layers was lower than that of *D. glomerata* practically independent of the growing season (Figs 48 & 50). This was due mainly to the shorter leaves of *F. pratensis* compared to *D. glomerata* in interspecific shoot competition (Fig. 46) and to its generally lower total leaf area per plant (Fig. 45).

In a dense canopy, most of the radiation is absorbed by the uppermost leaves (Caldwell 1987; Barnes et al. 1990). Our results emphasise the general view that the ability of one grass species to overtop another leads to considerable advantages in competition for light (e.g. Berendse 1989; Akey, Jurik & Dekker 1990; Holt 1995).

In intraspecific shoot competition, differences in average leaf size and leaf length increased drastically during the second half of the growth cycle in vegetative swards. This contrasting refoliation explained the consistently smaller leaves and the lower LAR of *F. pratensis* at the end of either growth cycles in vegetative swards independent of the year (Figs 46 & 47). This species-specific refoliation in intraspecific shoot competition towards the end of regrowth was caused mainly by differences in self-shading and leaf attributes (Part III). It might also be related to a relatively slow leaf elongation of *F. pratensis* at higher temperatures (Jelmini & Nösberger 1978A).

In response to interspecific shoot competition, *F. pratensis* increased its average leaf size, leaf length, and LAR (Figs 46 & 47). In contrast, the leaf size, leaf length, and LAR of *D. glomerata* were lower than in intraspecific shoot competition. Due to this contrasting response, both grasses reached a similar LAR in mutual competition for light. Nevertheless, *D. glomerata* had a higher total leaf area and considerably bigger and longer leaves in interspecific shoot competition than *F. pratensis* due to its generally higher SLA. In addition, the
response of leaf attributes of *F. pratensis* was probably limited by its inferior ability to adapt SLA to changes in light as compared to *D. glomerata* (Fig. 6, page 37). As a consequence, the leaf growth of *F. pratensis* in interspecific shoot competition could not compensate for its inherently lower SLA, confirming the importance of a high SLA in plant competition.

### 5.2 Contrasting response of regrowth after defoliation

Regrowth of *F. pratensis* in interspecific shoot competition was considerably slower than that of *D. glomerata* after the reproductive growth cycle in 1994 (Fig. 43A). This was caused both by the contrasting regrowth rate of both species in intraspecific shoot competition and by the effects of interspecific shoot competition. The lower regrowth rate of *F. pratensis* in intraspecific shoot competition was mainly the result of its lower proportion of remaining vegetative tillers after defoliation (Table 5, page 102).

Interspecific shoot competition had contrasting effects on shoot growth of both species after defoliation, manifested as a sharp decrease in Cb₅₀ of *F. pratensis* relative to *D. glomerata* during the first week of regrowth (Fig. 44). The most important parameter, therefore, was the reduced refoliation of *F. pratensis* as compared to refoliation in intraspecific shoot competition. As a result, *F. pratensis* had a notably lower leaf area and LAR than in intraspecific shoot competition 11 days after defoliation (Figs 45 & 47). In contrast, refoliation of *D. glomerata* was not affected. The slower initial refoliation strongly reduced the shoot competitive ability of *F. pratensis* during the second growth cycle, since *D. glomerata* reached a higher relative leaf area density already at the very beginning of the regrowth period (Fig. 48).

Both grasses responded to interspecific shoot competition with a similar reduction in the content of WSC in stubbles at the first defoliation in 1994 (Fig. 52). Despite this similar response, the content of WSC reserves in *F. pratensis* (35 mg) was very low as compared to *D. glomerata* (74 mg). In addition, *F. pratensis* responded to interspecific shoot competition with a significant increase in shoot weight ratio (Fig. 16, page 65), while the shoot weight ratio of
D. glomerata was not affected. This resulted in a 14% lower stubble weight ratio in F. pratensis and was one reason for a 41% lower stubble dry weight than in D. glomerata. The proportion of reproductive tillers at the first defoliation was not affected by shoot competition.

Similar to these results, reduced stubble and root dry weights and WSC contents, but unaffected herbage production, were found for shaded Lolium perenne and Festuca arundinacea swards (Thomas and Davies 1978; Grant, Barthram & Torvell 1981; Allard, Nelson & Pallardy 1991). Despite similar shoot yields, early growth of foliage after defoliation was reduced compared to unshaded swards due to the depleted WSC content of the stubbles. In line with these results, the lower availability of C probably explained to a large extent the slower initial refoiliation of F. pratensis in shoot competition with D. glomerata, since there was no remaining green leaf area after defoliation.

With increasing shading during regrowth in interspecific shoot competition the recovery of WSC reserves in F. pratensis was slowed down which, in turn, further reduced the availability of C during summer in both years (Fig. 52).

In 1994, the contrasting WSC contents of both species slightly affected initial shoot growth in subsequent growth cycles (Fig. 44). In 1995, the lower WSC contents during the summer did not limit the shoot growth of F. pratensis, probably due to the higher remaining leaf area per plant (6.2 cm²) as compared to D. glomerata (2.7 cm²). Hence, refoiliation of F. pratensis in interspecific shoot competition was similar to D. glomerata or even higher during the first week of regrowth (Fig. 50).

5.3 Contrasting interpretation of shoot competitive ability

Only a small number of field experiments on shoot competition with regularly defoliated pasture plants have lasted long enough to study the seasonal changes in shoot competition (Remison & Snaydon 1980; Martin & Field 1984; Carlen 1994). In addition, these studies focused on the response of above-ground attributes to shoot competition only and were not suitable for studying the whole plant response or the changes in response to shoot competition during regrowth.
Despite decreasing shoot competitive ability, Cb_{sh} of *F. pratensis* relative to *D. glomerata* increased during regrowth in June and August, while Cb_{st} and Cb_{r} decreased progressively towards the end of regrowth (Fig. 44). This contrasting response led to a significantly higher Cb_{sh} than Cb_{st}, Cb_{r}, and Cb, until the defoliation in August of both years. Hence, shoot competition only slightly affected shoot yield but strongly affected stubble and root dry weight of both species. These contrasting effects were the result of the opposing change in biomass allocation during regrowth in response to shoot competition. In interspecific shoot competition, the harvest index of *F. pratensis* increased significantly as compared to intraspecific shoot competition, while *D. glomerata* responded in the opposite manner (Fig. 51). In consequence, *F. pratensis* reached a higher harvest index in shoot competition with *D. glomerata*, while the opposite was true for intraspecific shoot competition.

*F. pratensis*, the weaker shoot competitor, obviously tried to increase its interception of above-ground resources by increasing its biomass allocation to shoot growth, while neglecting root and stubble growth. This strategy was ineffectual, since *F. pratensis* was still shaded by *D. glomerata* in interspecific shoot competition. In contrast, *D. glomerata* increased biomass allocation for root and stubble growth in response to the increasing availability of light in competition with *F. pratensis*.

Such a contrasting response of biomass allocation to the changed quantity and quality of light in both species is quite common and has been reported before (e.g. Thomas and Davies 1978; Givnish 1988; Allard, Nelson & Pallardy 1991). However, no information is available on the consequences of these contrasting responses for interpreting shoot competitive ability. In 1994, Cb_{sh} suggested a similar shoot competitive ability of both species at the end of each regrowth period from June to August. In fact, the shoot competitive ability of *F. pratensis* relative to *D. glomerata* decreased progressively due to the contrasting response of stubble and root growth in both species. In August 1995, Cb_{sh} still suggested a shoot competitive ability of -0.15 of *F. pratensis* relative to *D. glomerata*, while its effective shoot competitive ability, based on total dry weight, was clearly lower (Cb_{t} -0.52). These results demonstrate convincingly that the shoot
competitive ability based on shoot dry weight does not a priori reflect the whole plant response. Hence, an interpretation of shoot competitive ability based on shoot dry weight may be misleading. Experiments on shoot competition in pasture plants, focusing on the whole plant response seem to be more reliable and provide a better insight into processes in shoot competition.

Due to the trade-off in biomass allocation to shoots and roots, shoot competition affected above-ground and below-ground plant traits and, thus, root competition too. For *F. pratensis* this shift in biomass allocation resulted in a significantly lower total root dry weight in competition with *D. glomerata* in summer 1995 (Table 9). The increasing effects on root mass at higher soil depths in addition to the generally low root activity (Fig. 22, page 78) reduced the ability of *F. pratensis* to compete for nutrients and water. In a permanent grassland, this probably had further reduced its shoot competitive ability which, in turn, would have further reduced its root competitive ability.

The negative effects of the low shoot competitive ability of *F. pratensis* during summer were not compensated by the benefit of the relatively high competitive ability during reproductive growth in 1994 and in autumn of both years (Fig. 12, page 59). Hence, the period from June to the end of August was most important for the shoot competitive ability of *F. pratensis* relative to *D. glomerata*. The various seasonal effects of shoot competition and the changing response of plant attributes during regrowth indicate, however, that the response of pasture plants to shoot competition must be studied over a longer period.
5.4 Conclusions

In interspecific shoot competition, *F. pratensis* increased its average leaf size, leaf length, and LAR, while *D. glomerata* showed the opposite response. Despite this contrasting response, *D. glomerata* still reached a higher average leaf size and leaf length and overtopped *F. pratensis* after about three weeks of regrowth. Thus, increasing shading towards the end of regrowth during the vegetative phase was the major limitation of shoot competitive ability of *F. pratensis*.

Depending on the season, shading of *F. pratensis* could be explained by a combination of (i) a limited response of leaf attributes to shoot competition which could not compensate for differences in SLA, (ii) a lower regrowth rate after the reproductive growth cycle, and (iii) a reduced shoot growth after defoliation due to previous shading.

In interspecific shoot competition, *F. pratensis* increased shoot growth towards the end of regrowth at the expense of root and stubble growth. In contrast, *D. glomerata* increased root and stubble growth. The contrasting responses led first to a similar competitive ability based on shoot weight production but to a fast declining competitive ability expressed by the total dry weight of the plants. Hence, the shoot competitive ability, based on shoot dry weight, does not a priori reflect the whole plant response.
PART V

ARE ROOT APHIDS (G. SETULOSA) INVOLVED IN THE DECREASE OF FESTUCA PRATENSIS IN PERMANENT GRASSLANDS?

1. INTRODUCTION

Aphids that feed on roots (root aphids) were reported to have a substantial economic significance for lettuce (Kahrer 1987; Ciampolini et al 1993), sugarbeet (Summers & Newton 1989), sugarcane (Setokuchi 1993), rice (Yano, Miyake & Eastop 1983), and soybean (Oku & Miyahara 1982). They may also cause serious damage to wheat in the Middle East and the Third World (Mustafa & Akkawi 1987).

Root aphids such as Geoica setulosa (Pass., 1860) also attack the roots of forage grasses (Lampel & Meier 1995). In permanent grasslands and leys, such injuries usually go unnoticed. Hence, to the best of our knowledge, no qualitative information is available on the impact of root aphids on physiological and morphological plant traits of forage grasses.

The proportion of Festuca pratensis Huds. (Meadow fescue), a weak competitor under intensive management, drastically decreased during the past century. In a field study on the impact of season and shoot competition on above-ground and below-ground plant traits, F. pratensis was attacked by root aphids. In contrast, Dactylis glomerata (Orchard grass), its competitive counterpart, remained uninjured.

We analysed the impact of root aphids on the regrowth of F. pratensis after defoliation as well as on the content and restoration of water soluble carbohydrates (WSC) during regrowth.
2. MATERIALS AND METHODS

Infection of *F. pratensis* by root aphids

Swards of *F. pratensis* in intraspecific shoot competition were established in the field in October 1993 and defoliated monthly after 20 May 1994. The plots were irrigated during summer, and thus water did not limit growth.

The infection by root aphids occurred spontaneously in summer 1994. The species was identified by Lampel as *Geoica setulosa* Pass. The first symptoms on the roots of *F. pratensis* were observed on 21 June. The population of aphids drastically increased after the middle of July but did not affect the dry weight of above- and below-ground plant parts or percentage or content of water soluble carbohydrates until 21 July 1994.

*Geoica setulosa*

*Geoica setulosa* are off-white or pale, almost globular aphids covered by wax. They feed on the roots of forage grasses (*Alopecurus* spp, *Holcus* spp, *Festuca* spp, and *Poa* spp) or other grass species in central Europe, Italy, Iran, and Turkey (Lampel & Meier 1995). In Iran there is a holocycle with *Pistacia khinjuk STOCKS* as the primary host. In Europe *G. setulosa* is exclusively anholocyclic. *G. setulosa* is associated with ants, often overwintering in the nests of *Lasius flavus* (Godske 1992; Lampel & Meier 1995). After the beginning of March, they live outside of these nests on the roots of grasses.

Figure 54 shows the typical symptoms found on the roots of *F. pratensis* in intraspecific shoot competition in August 1994 in a sward infected by *G. setulosa*. The aphids are partly covered by waxy exudes.

Measurements

Fully destructive sequential harvests were made to determine the impact of root aphids on regrowth in swards of *F. pratensis* in intraspecific shoot competition after defoliation on 21 July 1994. Sequential harvests of the swards were made on the day of defoliation (0) and after five, 11, 19, and 28 days of regrowth. At each
harvest, two replicates of eight infected plants were compared with two replicates of eight uninfected plants. The impact of root aphids on the dry weight of the shoots, the stubble and root fraction, as well as on the content and restoration of WSC reserves were assessed at each harvest.

Figure 54: Roots infected by root aphids (Geoica setulosa) in a sward of F. pratensis in intraspecific shoot competition in August 1994. The infection by G. setulosa occurred spontaneously. First symptoms on the roots of F. pratensis were observed on 21 June 1994.

Treatments with insecticides

Both plots were treated with insecticides on the 24 August and the 7 September 1994 (223 mg/m² Pirimicarp dissolved in 900 ml H₂O, Pirimor, Maag AG, Dielsdorf, Switzerland). After the treatment, the swards were sprinkled with 1200 ml H₂O to bring the pirimicarp into deeper soil layers.
3. RESULTS

Dry weights of stubbles, roots, and the total remaining dry weight of infected plants were similar to the control at the defoliation of the swards on 21 July 1994 (Fig. 55). In contrast, regrowth of *F. pratensis* after defoliation in swards infected by *G. setulosa* was severely hampered as compared to the control.

Figure 55: Impact of root aphids (*Geoica setulosa*) on regrowth after defoliation in a sward of *Festuca pratensis* in intraspecific shoot competition. The course of Ln-transformed shoot dry weight (A), stubble dry weight (B), root dry weight (C), and total dry weight (D) of uninfected controls are compared to infected plants. The infection by *Geoica setulosa* occurred spontaneously. Means of two replicates at defoliation on 21 July, 15 August, and 15 September 1994 as well as after five, 11, and 19 days of regrowth after 21 July 1994 are shown. The swards were irrigated so that water did not limit growth. ▼ indicates the date of the treatment with insecticides. (I) stands for the standard errors.
Shoot growth of infested plants was unaffected for the first three weeks of the growth cycle (Fig. 55A). At the end of the growth cycle on 18 August, the shoot weight of infested plants (1859 mg plant\(^{-1}\)) was, however, severely reduced as compared to the control (2532 mg). The shoot yield of infested plants did not recover during the following growth cycle, despite the treatments with pirimicarp. Root aphids drastically reduced stubble and root growth of infested plants. Significantly lower stubble dry weights of infested plants were observed after the first week of regrowth (Fig. 55B). Similarly, lower root dry weights occurred after about two weeks of the growth cycle (Fig. 55C).

The total dry weight was reduced by 27%, attributable to the root aphids, at the defoliation on 18 August and reached 30% at the end of the following growth cycle (Fig. 55D).

The contents and concentrations of WSC in stubbles of infested plants decreased strongly after defoliation and did not recover until the end of the growth cycle (Figs 56A & C). Within only one growth cycle, the contents (61%) and concentrations (46%) of WSC in infested swards was reduced drastically as compared to uninfested swards due to the feeding of the aphids on the roots. During the subsequent growth cycle, concentrations of WSC in infested swards recovered to the same as in their uninfested counterparts, due probably to the treatments with insecticides. Though, the content of WSC in stubbles of infested plants (106 mg) was still 31% lower than in uninfested plants on 15 September due to the reduced stubble weight.

Similarly, the contents and concentrations of WSC in the roots of infested plants were strongly depleted within a short period of time (Figs 56B & D). In contrast to the WSC contents in stubbles, the concentration of carbohydrates in roots did not recover after applying the insecticides. Despite the severe reduction, the depleted WSC contents in stubbles and roots only partly accounted for the lower dry weight increase in infested plants than in their uninfested counterparts.
Figure 56: Impact of root aphids (Geoica setulosa) on the availability of carbohydrates during regrowth after defoliation in a sward of Festuca pratensis in intraspecific shoot competition. The contents (A & B) and concentrations (C & D) of water soluble carbohydrates (WSC) in stubbles (A & C) and roots (B & D) of uninfected controls are compared to infected plants. The infection by Geoica setulosa occurred spontaneously. Means of two replicates at defoliation on 21 July, 15 August, and 15 September 1994 as well as after five, 11, and 19 days of regrowth after 21 July 1994 are shown. The swards were irrigated so that water did not limit growth. ▼ indicates the date of the treatment with insecticides. (I) stands for the standard errors.
4. DISCUSSION

The infection by *G. setulosa* severely reduced the dry weight accumulation and the restoration of WSC reserves in *F. pratensis* during regrowth after defoliation (Figs 55 & 56). Since the plots were irrigated, the strongly reduced growth of infested plants was probably due to a lower efficiency in water and nutrient acquisition and to losses of assimilates by the roots, induced by the feeding of the root aphids.

In contrast to *F. pratensis*, *D. glomerata* the competitive counterpart, was not infested. The drastically lower regrowth capacity of *F. pratensis* infested by *G. setulosa* strongly reduced its competitive ability against uninfested species such as *D. glomerata*. As a result of the losses of assimilates and the severely reduced growth, infected plants may not have survived in a permanent grassland. Nevertheless, the high susceptibility to root aphids cannot account for the lower shoot competitive ability of *F. pratensis* in comparison to *D. glomerata* reported previously (Chapter II to IV), since infested plants were consequently excluded from analyses in these experiments. In 1995, the plots were treated regularly with pirimicarp to prevent *F. pratensis* being infected by *G. setulosa*.

*G. setulosa* is widely spread in Europe, but has, thus far, been observed only once in Switzerland (Passerini 1860). Root aphids have also been found on the roots of *F. pratensis* in permanent grasslands in the surroundings of Eschikon (Switzerland) in the summer of 1994 and 1995. The presence of root aphids in permanent grasslands is probably normally not detected because of their subterranean habit. Schmidt (1991) reported that *F. pratensis* was highly susceptible to *Aploneura lentisci*, which also feeds on the roots of infested plants. They reported that *F. pratensis* is frequently infected by *A. lentisci* in the soils of Changins (Switzerland) which may lead to plants dying in periods of dryness. Hence, *F. pratensis* may be generally more susceptible to root aphids than its companion grasses such as *D. glomerata*.

Cultivars of *F. pratensis*, infected by endophytes (*N. uncinatum*) were less susceptible to infection by *A. lentisci*. If the lower susceptibility accounts of *G. setulosa* too, that may to some extent explain the high frequency of endophyte-
infected *F. pratensis* in permanent grasslands in Switzerland (Schmidt 1993). Though, this high frequency may also be due to the higher competitive ability of *F. pratensis* ecotypes infected by endophytes and their tolerance to drought as reported by Malinowski et al (1997).

*G. setulosa* is associated with ants, often overwintering in the nests of *Lasius flavus* and well adapted to warm temperatures (Godske 1992; Lampel & Meier 1995). Hence, the significance of *G. setulosa* for the persistence of *F. pratensis* may be higher in extensively managed permanent grassland in mild climates than in sown grasslands and at higher altitude. However, no information is available about the spreading of root aphids in permanent grasslands of Switzerland. Further research may provide knowledge of the spread of root aphids in pasture plants and their ecological significance for the decreased proportion of *F. pratensis* in permanent grasslands.
GENERAL CONCLUSIONS

RGR of *F. pratensis* at non-limiting nutrient supply under controlled conditions was lower than that of *D. glomerata* due to a lower and less responsive SLA. In the field, *F. pratensis* was a weaker shoot competitor than *D. glomerata*. Its shoot competitive ability varied considerably with season, being relatively high in spring and autumn but strongly decreasing from June to the end of August. The relatively high shoot competitive ability of *F. pratensis* in spring was explained by a higher RGR as compared to *D. glomerata* due to a faster increase in LAR, a higher NAR, and, in one year, a higher proportion of reproductive tillers.

During summer, *F. pratensis* was generally overtopped in interspecific shoot competition towards the end of regrowth due to its lower and less responsive SLA. In addition, the lower proportion of vegetative tillers strongly reduced RGR of the whole plant and the shoot competitive ability of *F. pratensis* during the second growth cycle. In contrast, if not affected by the proportion of vegetative tillers, a low RGR was the consequence but not the cause of its low shoot competitive ability during summer. Therefore, the inherently lower and less responsive SLA of *F. pratensis* played a major role in limiting its shoot competitive ability.

The compensation processes, responsible for the changed resource availability in interspecific shoot competition, affected growth, morphology, and biomass allocation of the whole plant. Due to the trade-off in biomass allocation to shoots and roots, shoot competitive ability, based on shoot dry weight only, did not reflect the whole plant response.

Though *F. pratensis* was suppressed, intensive defoliation was the most convenient system of management, since the contrasting leaf extension occurred only during the second half of the growth cycle. Hence, extensive management in highly fertile soils may result in a lower persistence of *F. pratensis* due to a prolonged period of shading.


References


References


References


CURRICULUM VITAE

1973 - 1976 Primarschule Uetendorf Berg
1976 - 1981 Sekundarschule Uetendorf
1981 - 1982 Landw. Berufsschule Yverdon
1983 Abschluss der Lehre als Landwirt
1984 Landw. Fähigkeitsausweis
1984 - 1987 Gymnasium Thun. Abschluss: Matura Typus C
1987 - 1992 Studium an der Abteilung Landwirtschaft. ETH-Zürich
1988 - 1992 Didaktische Zusatzausbildung. ETH Zürich
1992 - Fähigkeitsausweis für das Lehramt an Berufs- und
- Fachschulen und höheren Lehranstalten
- Diplom als Ing. Agr. ETH. Fachrichtung Pflanzen-
produktion.
1993 - 1997 Assistent und wissenschaftlicher Mitarbeiter am Institut für
Pflanzenwissenschaften. ETH Zürich
1994 Heirat mit Béatrice Wiedmer
1995 - 1997 Nachdiplomstudium in Betriebswissenschaften. BWI.
ETH Zürich
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