Effect of substrate pH and calcium concentration on growth, root development and competitive ability of *Poa trivialis* L. and *Holcus lanatus* L.

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Summary

On the limed plots of a long-term fertilization experiment in old permanent grassland the abundance of *Poa trivialis* increased in the course of time, whereas that of *Holcus lanatus* decreased.

To explain this difference in response to liming, the effect of substrate pH and calcium concentration on root development, growth and competitive ability of these species was studied in three soil and water culture experiments.

Poa was found to be much more sensitive than *Holcus*, especially to the combination of low pH and low calcium concentration; its rooting depth being strongly reduced, the roots being shorter and thinner.

In a competition experiment at a soil pH of 4.1 *Poa* rooted more superficially than *Holcus*, whereas the reverse was true at a soil pH of 7.5. In either case the species with the deepest root distribution was the better competitor.

It is concluded that the different response of these species to liming in the field experiment is to a large extent attributable to different sensitivity of root development to the combination of low pH and low calcium concentration, resulting in a different root distribution and, consequently, different ability to compete for resources, most probably for water.

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Introduction

In plant geography and ecology the calcium carbonate content of the soil is an important aspect. It is well-known that some plant species prefer calcareous soils, whereas others prefer acidic soils. The abundant literature on the ecophysiology of calcicole and calcifuge plants has recently been reviewed by Kinzel (1982).

In studying this problem it is important to realize that calcareous and acidic soils differ not only in their content of calcium carbonate, but also in many other properties that may be important to plant growth, such as the availability of nutrients, the concentration of toxic elements, the physical structure and biological activity in the soil.

In this paper we deal only with calcium and pH, but this does not mean that other factors are considered unimportant in the present case.

Results of a fertilization experiment on permanent grassland

In 1957 a fertilization experiment had been started at 'De Ossekampen', on an old extensively used grassland on heavy river-clay soil. It was intended to study the influence of management (pasture vs. hayfield) and various fertilizer combinations on the botanical composition and biomass production.

Remarkable results of this experiment were the increase in abundance of *Poa trivialis* on the limed pasture plots (receiving 1000 kg CaO ha⁻¹ year⁻¹) and its decrease on the unlimed pasture plots with a pH of 6.5 and 4.5 respectively. *Holcus lanatus* on the other hand decreased in importance on the limed pasture plots and maintained its position on the unlimed pasture plots. On all hayfield plots (pH 3.8) *Poa trivialis* and *Holcus lanatus* decreased sharply, with exception of *Poa trivialis* on the plots receiving lime (pH 6.6) (Elberse et al., 1983).

Over the last 20 years the experimental field had grown drier due to improved drainage in the whole area. The moisture-indicating species Agrostis canina, Cardamine pratensis, Carex panicea and Carex nigra declined considerably in most plots. Since Poa trivialis is also known as a moisture indicator (Kruijne et al., 1967; de Boer, 1956) its tendency to decline on most plots could be related to the lower ground-water level. The fact remains, however, that liming apparently reversed this tendency.

To study the differences in response of *Poa trivialis* and *Holcus lanatus* to liming some experiments have been carried out in a climate room. This paper deals with the effect of substrate pH and calcium concentration on root development, growth and competitive ability. To save repetition both species are referred to by their generic names only in the remainder of this paper.

Literature data on the lime response of Poa trivialis and Holcus lanatus

The difference in response to liming between *Poa* and *Holcus* observed at 'De Ossekampen' is corroborated by several other publications. Behaeghe et al. (1970) reported that the abundance of *Poa* in a fertilized grassland increased due to liming.

De Vries & Kruijne (1943) considered *Poa* a species with a moderate lime requirement. *Poa* showed a small positive response to lime, whereas *Holcus* disappeared from most of the limed plots of the Rothamsted Park Grass experiment (Williams, 1978). Hart & McGuire (1963) also found a negative response of *Holcus* to liming.

Comparable findings have been reported concerning the response of these species to soil pH. According to Kruijne et al. (1967) and Grime & Lloyd (1973) *Poa* prefers neutral soils (pH 5-7). Kruijne et al. (1967) reported a gradual decrease in importance of *Holcus* in Dutch grasslands going from pH 4 to pH 8. According to Grime & Lloyd (1973) *Holcus* occurs at a wide range of soil pH values with a sharp decline below pH 4. Remison (1976) found higher yields of *Holcus* at pH 4.0 than at pH 6.0. In the Rothamsted Park Grass experiment *Holcus* dominated in some of the unlimed acid subplots (pH 3.7). There were, however, also plots where the amount of *Holcus* increased by liming (Williams, 1978). Rogers & King (1972) found a weak positive relation between coverage of *Holcus* and soil pH. Davies (1944) reported the optimum pH range for *Holcus* to be between pH 5 and pH 7.5, although it occurred often as a pioneer species on soils with pH below this optimum range. In the Sheffield area *Holcus* was found on soil with pH between 3.5 and 8.0, but most frequently between 5.0 and 6.0 (Watt, 1978).

Summarizing these findings from the field it appears that *Poa* prefers neutral soils, showing a positive response to liming. *Holcus* appears to occur at a wide range of soil pH with an optimum at slightly acid soils. It mostly shows a negative response to liming.

Material and methods

The plant material used in the experiments described in this paper was obtained by vegetative reproduction from plants that had been collected on the experimental field 'De Ossekampen'.

Water culture experiment

Plants of *Poa* and *Holcus* were grown in water cultures in 6-litre enamel pots. The plants were fixed with strips of foam plastic in the holes of a plastic plate. The experiment included 5 calcium concentrations (0.25, 1.00, 1.75, 2.50, 3.25 meq l^{-1}) and two pH levels (approximately 3.7 and 6.7). The calcium concentrations were obtained by replacing Na by Ca, keeping the sum of Ca²⁺ and Na⁺ at 3.50 meq l^{-1} . The pH levels were obtained by adding H_3PO_4 and KOH. During the experiment the pH was regularly readjusted. The nutrient solution further contained (in meq l^{-1}) 2.10 K⁺, 1.40 Mg²⁺, 5.25 NO $_3^-$, 0.35 $H_2PO_4^-$, 1.40 SO $_4^{2-}$, Fe-EDTA and trace elements according to Hoagland & Arnon (1938). The solutions were renewed every fortnight. The experiment was carried out in triplicate in a climate room at 20 °C, 70 % relative humidity and a light intensity of 40 W m⁻² during 15 hours per day.

After 24, 42 and 68 days the shoots were clipped at 4 cm height. At the last date stubbles and roots were also harvested. Shoots, stubbles and roots were weighed and analysed for contents of K, Ca, Mg, Na, N, P and S.

Rooting experiments

Plants of *Poa* and *Holcus* were grown in frames designed for observation of roots growing in water cultures, and in rooting boxes designed for observation of roots growing in soil.

The experiment with root observation frames included 5 pH levels (3.7, 4.5, 5.5, 6.5 and 7.5) and 2 Ca levels (0.5 and 3.0 meq l^{-1}). The pH levels were obtained by adding H_2SO_4 or NaOH. The Ca levels were obtained by replacing Ca by K, Na and Mg in equal parts, giving the following compositions:

| | Ca ²⁺ | K+ | Mg^{2+} | Na+ | NO_3^- | $H_2PO_4^-$ | SO_4^{2-} |
|---------|------------------|------|-----------|------|----------|-------------|-------------|
| high Ca | 3.00 | 1.51 | 1.57 | 0.17 | 4.50 | 0.35 | 1.40 |
| low Ca | 0.50 | 2.35 | 2.40 | 1.00 | 4.50 | 0.35 | 1.40 |

Fe-EDTA and trace elements were added according to Hoagland & Arnon (1938).

The observation frames consisted of a perspex plate, a synthetic membrane permeable to water and solutes but not to roots (trade name Viledon), an irrigation mat providing equal distribution of the nutrient solution all over the membrane, and a perforated aluminium plate gently pressed together. Ten frames were placed vertically in a dark container, only the shoots of the plants were exposed to light. The experiment was carried out in a climate room at 18 °C, relative humidity of 70 %, illumination of 60 W m⁻² during 14 hours per day.

Each nutrient solution was supplied to the top of a root observation frame by a peristaltic pump at a rate of 2 l per day. After flowing through the frames the solutions were drained away. After one week pregrowth on the various treatment solutions one plant of each species was mounted with its roots between the perspex plate and the membrane of each observation frame. After 2, 3 and 4 weeks photographs were taken of the roots in the ten frames.

To compare the results of the above experiments on water culture with the response of roots to two different soil pHs, three plants of either species were grown at two pH levels (3.7 and 6.7) in glass-faced boxes containing a sandy soil, and placed in an inclined position (Böhm, 1979). The lower pH was obtained by adding H_2SO_4 . During the experiment the pH values remained constant. On 18 subsequent days, the daily root growth was recorded in different colours on a transparent foil that was attached to the observation side of each rooting box.

Competition experiment

Poa and Holcus were grown in monocultures and various mixtures in enamel 6-litre pots containing a sandy soil (7 kg air dry soil per pot), fertilized with 7 g per pot of pulverized fertilizer (12 % N, 10 % P, 18 % K). The plant densities of Poa/Holcus were 16/0, 14/2, 12/4, 8/8, 4/12, 2/14 and 0/16 plants per pot.

The experiment included two pH levels (4.1 and 7.5) and two moisture levels (normal and limited). The pH levels were obtained by mixing the soil with H_2SO_4 or $CaCO_3$. The normal moisture level received daily additions of water to field capacity. The limited moisture level was left to dry out until pF 4 was reached before adding water to field capacity.

The experiment was carried out in triplicate in a climate room at day/night tem-

peratures of 20/14 °C, 60 % relative humidity and of 40 W m $^{-2}$ during 15 hours per day.

Results

Water culture experiment

Yields. Fig. 1 shows that at pH 6.7 the yields of *Poa* and *Holcus* were considerably depressed only at the lowest Ca level of 0.25 meq l⁻¹. The yields of *Holcus* at the various Ca levels were hardly influenced by lowering the pH from 6.7 to 3.7, whereas the yields of *Poa* were considerably decreased, especially those at the intermediate Ca levels. Thus the sensitivity of *Poa* to low Ca concentrations appears to be increased by low pH.

Poa had a higher shoot/root ratio than Holcus (Table 1). At the lowest Ca concentration the shoot/root ratio of both species was somewhat increased as compared to the other Ca levels. The pH had no influence on the shoot/root ratio of Holcus. The shoot/root ratio of Poa was increased by approximately 30 % by low-

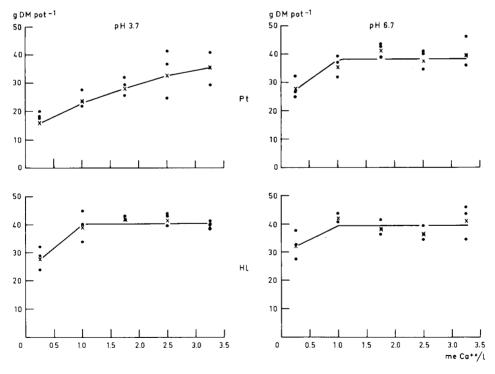


Fig. 1. Dry matter yields per pot of the whole plant at the last harvest of *Poa trivialis* (Pt) and *Holcus lanatus* (Hl) at pH 3.7 and pH 6.7 and various calcium concentrations in the nutrient solution (•, replicates, × means, corrected for foam plastic sticking to the roots).

J. R. VAN NIEUWENHUIZEN ET AL.

Table 1. Average shoot/root ratio of *Pao trivialis* and *Holcus lanatus* at pH 3.7 and pH 6.7 and different calcium concentrations in meq $Ca^{2+}l^{-1}$ (average of three replicates).

| | pH 3.7 | | | | | pH 6.7 | | | | |
|--------|--------|------|------|------|------|--------|------|------|------|------|
| | 0.25 | 1.00 | 1.75 | 2.50 | 3.25 | 0.25 | 1.00 | 1.75 | 2.50 | 3.25 |
| Poa | 13.0 | 10.5 | 9.7 | 9.6 | 10.1 | 8.5 | 7.4 | 8.3 | 6.6 | 7.8 |
| Holcus | 7.2 | 6.6 | 7.0 | 6.7 | 6.1 | 7.5 | 6.0 | 6.4 | 7.8 | 6.8 |

Table 2. Average number of tillers per pot of *Poa trivialis* and *Holcus lanatus* at pH 3.7 and pH 6.7 and different calcium concentrations in meq Ca^{2+} l⁻¹ (average of two replicates).

| | pH 3.7 | | | | | pH 6.7 | | | | |
|--------|--------|------|------|------|------|--------|------|------|------|------|
| | 0.25 | 1.00 | 1.75 | 2.50 | 3.25 | 0.25 | 1.00 | 1.75 | 2.50 | 3.25 |
| Poa | 555 | 808 | 819 | 925 | 1257 | 742 | 1005 | 928 | 1067 | 1113 |
| Holcus | 515 | 648 | 679 | 701 | 770 | 503 | 645 | 656 | 606 | 702 |

Table 3. Average fresh weight of one tiller (mg) of *Poa trivialis* and *Holcus lanatus* at pH 3.7 and pH 6.7 (average of two replicates and over all calcium levels).

| | pH 3.7 | pH 6.7 | |
|---------------|--------|--------|--|
| Poa | 100 | 158 | |
| Poa Holcus | 251 | 280 | |

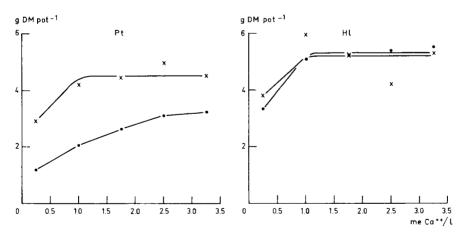


Fig. 2. Average dry matter yields of roots per pot at the last harvest of *Poa trivialis* and *Holcus lanatus* at pH 3.7 (\bullet) and pH 6.7 (\times) and various calcium concentrations in the nutrient solution.

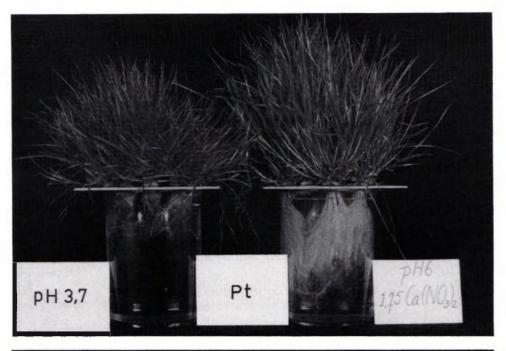




Fig. 3. Plants of *Poa trivialis* and *Holcus lanatus* grown in water culture at pH 3.7 and pH 6.7 and a calcium concentration of 1.75 meq Ca^{2+} I^{-1} . In contrast to *Poa*, *Holcus* does not show a difference in rooting depth.

ering the pH from 6.7 to 3.7, irrespective of the Ca level.

In general *Poa* had a higher number of tillers per pot (Table 2) but a lower weight per tiller than *Holcus* (Table 3). Tiller number of both species increased with increasing Ca level. Tiller weight showed not a clear relation to Ca level. Tiller number of *Poa* was higher at pH 6.7. Tiller number of *Holcus* did not depend on the pH. Tiller weight of both species was highest at pH 6.7.

The weight of the roots showed largely the same pattern as the weight of the whole plants (Fig. 2). Root growth of both species was considerably hampered at the lowest Ca level of 0.25 meq l⁻¹. Lowering the pH from 6.7 to 3.7 hardly affected root growth of *Holcus*, while it severely reduced growth of *Poa* at all Ca levels. Notably, the critical Ca concentration needed to prevent root growth reduction was increased from 1.0 to 2.5 meq l⁻¹ by lowering the pH.

Root morphology. Not only the root weight but also the morphology of the individual roots of *Poa* was changed by the treatments. At pH 3.7 the roots of *Poa* were short, thin, dark coloured with few lateral roots, apart from the many laterals growing above the surface of the culture solution (Fig. 3). The length of the lateral roots increased with increasing Ca concentration.

The roots of *Holcus* showed only small differences in morphology between treatments.

Chemical composition of the plants. In general Poa had the highest calcium concentration in the plants. The Ca concentration in the shoots of Holcus decreased from 350 to 50 meq kg⁻¹ with decreasing Ca concentration in the culture solution, those of Poa from 450 to 80 meq kg⁻¹. The Na concentration increased strongly due to the replacement of Ca by Na in the solution. The pH level of the solution had considerable influence on the chemical composition of the roots. At pH 3.7 the concentrations of Ca, K, Na and Mg were reduced by about 40 %.

Summarizing the results of this experiment it can be concluded that *Poa* and *Holcus* did not differ in sensitivity to low Ca concentration in the nutrient solution when the pH was about neutral. For both species the critical Ca²⁺ level to prevent root growth reduction was between 0.25 and 1.0 meq l⁻¹. Lowering the pH to 3.7 hardly affected the performance of *Holcus*, whereas *Poa* was strongly affected, including an increase in sensitivity to low Ca concentration (critical level 2.5 meq l⁻¹). Main effects of treatments were on total plant weight (including tiller number, tiller weight and root weight), on shoot/root ratio, on concentration of the cations in the plant and on depth and morphology of the roots of *Poa*.

Rooting experiments

From the root observation frames it appeared that the root systems of *Poa* and *Holcus* are rather different. In general *Poa* forms finely branched roots mainly concentrated in the top 10 cm, the deepest roots reaching only 20 cm after two weeks. Laterals develop shortly behind the top of main roots. *Holcus* produces thicker and longer main roots in the upper 20 cm, the deepest roots reaching 36 cm after two

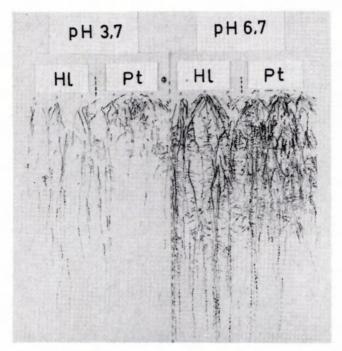


Fig. 4. Rooting of Poa trivialis and Holcus lanatus after 18 days in rooting boxes at pH 3.7 and pH 6.7.

weeks. Development of laterals starts 5 to 10 cm behind the tip of main roots.

Root development of both species was better at $3.0 \,\mathrm{meq}\,\mathrm{Ca^{2+}\,l^{-1}}$ than at $0.5 \,\mathrm{meq}\,\mathrm{Ca^{2+}\,l^{-1}}$. At the higher Ca level they produced more laterals per unit length of main root and the main roots as well as the laterals were longer. The length of the main roots of *Poa* increased with increasing pH, reaching an optimum at pH 6.5. Rooting depth of *Holcus* was less affected by pH, but the tendency was the same.

The observations on the roots in the rooting boxes showed the same difference between the species concerning their response to substrate pH (Fig. 4).

The treatments also affected the specific root length (Table 4). At pH 6.5 the species did not differ in this respect, both species having the highest specific length at the higher Ca level. At pH 4.5, *Poa* had the highest specific root length (meaning

Table 4. Average specific root length (in m g^{-1} fresh weight) of *Poa trivialis* and *Holcus lanatus* at pH 4.5 and pH 6.5 and two calcium concentrations in meq Ca^{2+} l^{-1} (average of two replicates).

| | pH 4.5 | pH 4.5 | | |
|--------|-------------|-------------|-------------|-------------------------|
| | 0.5 meq l-1 | 3.0 meq 1-1 | 0.5 meq l-1 | 3.0 meq l ⁻¹ |
| Poa | 20.9 | 22.2 | 11.8 | 19.5 |
| Holcus | 14.2 | 12.6 | 14.7 | 19.5 |

thinner roots). At this pH there was little influence of the Ca level on specific length.

Summarizing these results it is concluded that the main difference in root development between Poa and Holcus concerns their rooting depth, Holcus having the deeper roots. This difference increases on acid soils due to the greater sensitivity of Poa to low soil pH.

Competition experiment

Theory. The results of this experiment have been treated following the theoretical approach outlined by de Wit (1960) and de Wit & van den Bergh (1965). Curves have been fitted by hand to the yields of each species according to the hyperbolic functions:

$$O_{\rm p} = k_{\rm pH} \cdot z_{\rm p} (k_{\rm pH} \cdot z_{\rm p} + z_{\rm H})^{-1} M_{\rm p}$$
 (1a)

$$O_{\rm H} = k_{\rm HP} \cdot z_{\rm H} (k_{\rm HP} \cdot z_{\rm H} + z_{\rm P})^{-1} M_{\rm H} \tag{1b}$$

$$O_{H} = k_{HP} \cdot z_{H} (k_{HP} \cdot z_{H} + z_{P})^{-1} M_{H}$$

$$z_{P} = Z_{P} (Z_{P} + Z_{H})^{-1} \text{ and } z_{H} = Z_{H} (Z_{P} + Z_{H})^{-1}$$
(1b)
(1c)

in which

 $O_{\rm P}$ and $O_{\rm H}$ are the yields of *Poa* and *Holcus* in the mixtures

 $M_{\rm P}$ and $M_{\rm H}$ are their yields in the monocultures

 $z_{\rm p}$ and $z_{\rm H}$ are their relative plant frequencies at the start

 $Z_{\rm p}$ and $Z_{\rm H}$ are their absolute plant densities

 $k_{\rm PH}$ and $k_{\rm HP}$ are the relative crowding coefficients of *Poa* with respect to *Holcus* and vice versa

 $k_{\rm PH} > k_{\rm HP}$ means that *Poa* is the stronger competitor. When $k_{\rm PH} \times k_{\rm HP} = 1$ it can be concluded that the species compete for the same resources (no niche differentiation). In this case the sum of the relative yields (RYT) is unity:

$$RYT = r_{P} + r_{H} = O_{P}/M_{P} + O_{H}/M_{H} = 1$$
 (2)

The changes in the specifies composition of the mixtures are expressed in the relative replacement rate (o) calculated for the successive harvests with respect to the plant ratio at the start:

$$\varrho_{\rm PH} = (r_{\rm P}/r_{\rm H})/(Z_{\rm P}/Z_{\rm H})$$
 (3)

 $\varrho_{\rm PH} > 1$ means that *Poa* was the stronger competitor in the period concerned.

Results. The results of the competition experiment are summarized in Table 5. A good impression of the course of the competition is obtained by plotting the relative replacement rates (ρ) for the subsequent harvests against time (Fig. 5). It can be seen that Poa is rapidly crowded out by Holcus at the lower soil pH, whereas Poa is the stronger competitor at the higher soil pH. The competitive relations have not been changed essentially by varying the moisture level in this potexperiment. The kvalues in Table 5 show the same trend.

The reason for this remarkable change in competitive relations due to soil pH can be inferred from Figure 6, where the vertical root distribution in the monocultures

| | pH 4.1 | | | | pH 7.5 | | | |
|----------------------|------------|------|------|------|--------|------|------|------|
| Harvest | 1 | 2 | 3 | 4 | 1 | 2 | 3 | 4 |
| Normal moi | sture supp | ly | | | | | | |
| RYT | 1.00 | 0.89 | 0.97 | 1.00 | 0.99 | 0.98 | 0.94 | 1.08 |
| $k_{	ext{PH}}$ | 1.00 | 0.68 | 0.33 | 0.16 | 1.59 | 2.76 | 2.37 | 3.54 |
| $k_{\rm HP}$ | 1.00 | 1.04 | 2.75 | 6.20 | 0.63 | 0.32 | 0.39 | 0.41 |
| $\varrho_{	ext{PH}}$ | 1.00 | 0.82 | 0.34 | 0.18 | 1.53 | 3.08 | 2.50 | 2.75 |
| Limited moi | sture supp | ly | | | | | | |
| RYT | 0.91 | 1.05 | 1.14 | 1.05 | 1.13 | 0.99 | 1.02 | 1.05 |
| $k_{\mathtt{PH}}$ | 1.27 | 0.55 | 0.41 | 0.29 | 1.00 | 1.41 | 1.42 | 1.62 |
| $k_{\rm HP}$ | 0.48 | 3.19 | 3.21 | 4.07 | 1.50 | 0.61 | 0.80 | 0.55 |
| $\varrho_{	ext{PH}}$ | 0.60 | 0.48 | 0.50 | 0.23 | 1.30 | 1.55 | 1.50 | 1.80 |

Table 5. Values of RYT (at z = 0.5), $k_{\rm PH}$, $k_{\rm HP}$ and $\varrho_{\rm PH}$ (at z = 0.5) are obtained by fitting the functions (2), (1) and (3) respectively to the observed above ground yields at the successive harvest times.

of *Poa* and *Holcus* at normal moisture supply is presented. At pH 4.1 the major part (85 %) of the roots of *Poa* was concentrated in the uppermost 5 cm of the soil, while *Holcus* rooted mainly in the deeper soil layers (45 % above 5 cm). At pH 7.5 *Poa* rooted less superficially (only 55 % above 5 cm), whereas most roots of *Holcus* were in the upper 5 cm (70 %). Thus it appears that in either case the deepest rooting species was the stronger competitor.

The treatment with the limited moisture supply shows to a less extent the same trend.

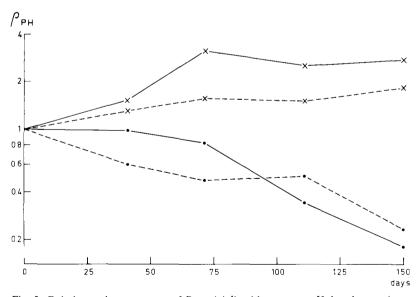


Fig. 5. Relative replacement rate of *Poa trivialis* with respect to *Holcus lanatus* (ϱ_{PH} at $z_P = z_H = 0.5$) plotted logarithmically against time at pH 4.1 (\bullet) and pH 7.5 (\times) and normal (---) and limited (- - -) moisture supply.

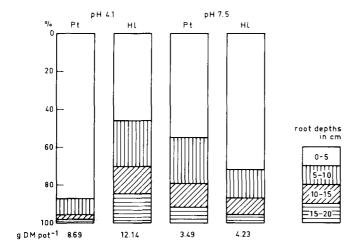


Fig. 6. Percentual distribution of the root dry matter yield per soil layer of 5 cm of monocultures of *Poa trivialis* and *Holcus lanatus* at pH 4.1 and pH 7.5 and normal moisture supply at the fourth harvest (average of two replicates).

Table 5 shows that the RYT values of the different treatments did not differ systematically from unity. From this it can be inferred that the differences in rooting depth have not lead to niche differentiation between the species in this experiment.

Summarizing the results we may conclude that the pH of the soil has determined the course of the competition between *Poa* and *Holcus* by its differential influence on the root development of these species.

Discussion

Most effects of substrate pH and Ca concentration on the various aspects of plant performance as observed in the present experiments have been described already for other species (cf. reviews by Foy, 1974; Moore, 1974; Kinzel, 1982).

Insufficient Ca supply is known to interfere with the functioning of roots, because low degrees of saturation of roots with calcium cause instability of cell membranes and consequent problems with uptake and transport of nutrients and water and excluding toxic substances. Since Ca is important in the formation of cell walls insufficient supply also causes damage in the meristems of roots and shoots. The observed differences between *Poa* and *Holcus* in sensitivity to low Ca concentrations could be caused by differences in affinity to Ca of the exchange sites on their roots.

Since direct effects of low substrate pH on plant performance occur mainly below pH 3.0, effects that have occurred in the present experiments will have been mostly indirect. Possible indirect effects are changes in the solubility of nutrients and toxic elements in the soil, competitive interaction of protons with cation uptake and exchange of cations absorbed on the roots.

In the present experiments replacement of absorbed Ca ions may have caused Ca

deficiency, consequent instability of cell membranes and eventually death of the root meristems. Apart from interference of protons with Ca nutrition, there must have been other effects of pH, because root length of *Poa* was reduced by low pH at low as well as high Ca levels (Fig. 3 and 4). Some other effects of low pH on root growth must have occurred, but the available information gives us no clues as to its nature.

When comparing the root yields of the water culture experiment with the root yields of the competition experiment (soil culture, see Fig. 6), it is striking that in the latter the highest root yields of both species were obtained at the lower pH (4.1), whereas in the water culture experiment the root yield of *Poa* (not of *Holcus*) was lowest at the lowest pH (3.7). One explanation could be that between pH 4.1 and pH 3.7 a very steep reduction in root yield occurs. Findings of Wind (1967) point to such a reduction. The lower yields at pH 7.5 in the competition experiment could also be due to increased decomposition of the roots at this high soil pH (Troughton, 1957), the more so because this experiment lasted for 150 days, which is relatively long.

In none of the present experiments Ca deficiency symptoms have been observed in the shoots of either species, not even at the lowest Ca level of 0.25 meq l⁻¹ in water culture. Evidently, the Ca concentrations in the shoots of *Poa* and *Holcus*, which were about 80 and 50 meq kg⁻¹ respectively, at this lowest level, come up to the functional requirement for shoot growth. The concurrent yield reduction probably resulted from failure of the roots. At the next higher Ca level (1.0 meq l⁻¹) Ca concentrations in the shoots of *Poa* and *Holcus* were about 180 and 140 meq kg⁻¹ respectively. Since there was no growth reduction (except for *Poa* at pH 3.7) these concentrations indicate sufficient Ca supply, provided that there is no depletion around the roots.

According to Dirven (1984) average Ca concentrations in *Poa* and *Holcus* in the field are about 305 and 270 meq kg⁻¹, which suggests that yield reduction due to insufficient Ca supply is not to be expected in the field. It may be, however, that slight disfunctioning of roots, that does not lead to growth reduction in water culture, aggravates specific problems occurring in the field, such as water stress, aluminium toxicity and competition by other species.

The present experiments have added to our understanding of the changes in abundance of *Poa* and *Holcus* in the field in relation to the application of lime, revealing an intricate interplay of factors. The abundance of *Poa* at the start of the fertilization experiment at 'De Ossekampen' agrees with its known preference for moist soil conditions and pasture management (Kruijne et al., 1967; de Boer, 1956). Its decline on most of the plots is probably due to the combination of its poor adaptation to the prevailing moderately acid soil conditions (acidity even increased slightly on most plots; see Elberse et al., 1983), the change of management on the hayfield plots and the improved drainage in the area. Due to its shallow root system especially in acid conditions *Poa* will have suffered from water stress more often than species like *Holcus*. Even if this would not have been fatal to *Poa* when living in isolation, it will have affected its competitive ability, resulting in a gradual replacement by other species.

The application of lime will have resulted in a deeper root system of *Poa*, compensating for the dryer conditions. The results of the competition experiment also indicate that *Holcus* is affected by the increase in pH, though the reason for this remains obscure. As a result the competitive relations have changed to the benefit of *Poa* far enough to maintain and even increase its frequency on the limed plots.

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