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Influence of water conditions on growth and mineral nutrient uptake of native plants on calcareous soil

Aparna Misra

Academic dissertation for the degree of Doctor of Philosophy, to be publicly defended in Blå Hallen at the Department of Ecology, Plant Ecology and Systematics, Ecology Building, Sölvegatan 37, Lund on September 5th, 2003 at 10.00 a.m., by the permission of the Faculty of Natural Science of Lund University.

The thesis will be defended in English

Faculty opponent: **Prof Olof Andréén**, Department of Soil Science, SLU , Uppsala, Sweden.

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Abstract <p>The studies presented in Papers I to IV illustrate the importance of soil moisture in soil solution chemistry and response of native plants to the changes induced by change in moisture regime. With the help of glasshouse experiments I tried to study the influence of different treatments of soil moisture conditions on the mineral uptake by native plants of calcareous soil. I also tried to find the correlation between response of the studied species to soil moisture and their field conditions on Öland.</p> <p>Change in moisture level in the soil influenced plant nutrition, which was relevant both in the field and in the greenhouse. I studied different soil moisture conditions held at constant level and also wet/dry fluctuations. Soil moisture had a profound effect on pH and concentrations of several ions like HCO₃, Ca, Mg, K, P, Mn, Zn. Soil moisture affects mineral uptake directly by changing soil solution concentrations of certain ions, such as Ca, Mg, K, or indirectly by changing pH and HCO₃. Bicarbonate and pH increased with increasing soil moisture, being closely correlated to each other. I observed increase in solubility of P and Mn with increasing moisture level, elements that are considered as limiting factors on calcareous soil. Zinc concentration in soil solution was adversely affected by increasing soil moisture. It is concluded that variation in soil moisture can influence the distribution of dry and wet growing species by affecting soil solution chemistry. Plants responded more or less according to their field conditions. The studies presented in my thesis indicated that soil moisture plays an important role, influencing soil solution chemistry and nutrient uptake by plants.</p>		
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A doctoral thesis at a university in Sweden is produced either as a monograph or as a collection of papers. In the latter case, the introductory part constitutes the formal thesis, which summarises the accompanying papers. These have either already been published or are manuscripts at various stages (i.e. in press, submitted, or manuscript).

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Dedicated to

My parents

&

parents in law

Mrs. Pushpa Tripathi and Mr. Ashok Kumar Tripathi Mrs Shushila Misra and Mr. Gopal Krishna Misra

Papers

This thesis is based on four papers, which are referred to by their Roman numerals (I-IV)

- I Misra, A. and Tyler, G. **1999**. Influence of soil moisture on soil solution chemistry and concentrations of minerals in the calcicoles *Phleum phleoides* and *Veronica spicata* grown on a limestone soil. **Annals of Botany 84: 401-410.**
- II Misra, A. and Tyler, G. **2000**. Effect of soil moisture on soil solution chemistry, biomass production, and shoot nutrients in two native grasses on a calcareous soil. **Communications in Soil Science and Plant Analysis 31: 2727-2738.**
- III Misra, A. and Tyler, G. **2000**. Effects of wet and dry cycles in calcareous soil on mineral nutrient uptake of two grasses, *Agrostis stolonifera* L. and *Festuca ovina* L. **Plant and Soil 224: 297-303.**
- IV Misra, A. **2003**. Influence of soil moisture on nutrient concentrations in, and competition between species on limestone soil. **Manuscript, 19 pp.**

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Sammanfattning

Studierna som presenteras i paper I till IV i min avhandling visar markvattnets betydelse för marklösningens kemi och växternas respons på förändringen i vattenhalt. Med mina experiment har jag studerat dels kalkjord med olika vattenhalter och dels markvattens påverkan på växternas näringsupptagning i växthus. Jag har också försökt finna samband mellan växternas respons på markfuktigheten och deras fördelning på Ölands alvar.

Variationer i markfuktigheten påverkade växternas näringsupptagning både i växthusexperiment och i fält. En förändring av markfuktigheten påverkade tillväxten och var av betydelse för växternas möjlighet att ta upp den näring som de behöver för sin produktion. Jag har undersökt betydelsen av olika konstant markfuktighet men även av varierande markfuktighet.

Mina studier visar att variationer i markens vattenhalt är särskilt betydelsefulla för pH och lösligheten av olika joner som HCO_3 , Ca, Mg, K, P, Mn och Zn. Markfuktigheten påverkar upptaget av mineraler dels genom att koncentrationerna av Ca, Mg och K, och dels genom att pH and HCO_3 koncentrationen i marklösningen förändras. Bikarbonathalten och pH är korrelerade och ökar då markfuktigheten ökar. Jag observerade en ökning i P- and Mn-koncentrationerna i marklösningen vilka betraktas som begränsande faktorer i kalkjord. Zinkkoncentrationen i marklösningen minskade däremot då markfuktigheten ökade. Min slutsats är, att variationer i markfuktighet kan påverka fördelningen av växter anpassade till torra respektive fuktiga markförhållanden beroende på variationer i marklösningens kemi. Studierna presenterade i min avhandling visar, att markfuktighet spelar en viktig roll för marklösningens kemi och näringsupptagningen i växterna.

Contents of the formal thesis

<i>Introduction</i>	12
<i>Hypotheses and objectives</i>	15
<i>Main findings</i>	16
Effect of moisture on soil solution concentration	16
pH and bicarbonate	18
Calcium and magnesium	19
Phosphorus	19
Zinc and manganese	20
Other nutrients	21
Response of plants to the changes influenced by soil moisture	22
Preferably dry growing species	22
Preferably wet growing species	28
<i>Discussion</i>	30
<i>Main conclusions</i>	33
<i>References</i>	34

Introduction

The ecological conditions characterizing calcareous soils impose several severe ecological demands on plant life. Plants must be able to tolerate periods of strong drought during the summer, but also periods of water submersion during the winter half of the year, due to impeded drainage where the bedrock is uncracked and shallow.

Soil regimes have an important limiting and regulatory role in the vital activity of various organisms (Dmitriev, 1997). Soil moisture is the most important factor separating the wet-moist communities in semi-natural meadows in southern Sweden (Linusson et al., 1998). Especially on the Alvar of Öland, the relationship between the small-scale species distribution and soil depth was documented by Tyler (1999). Species, which are unable to withstand periods of severe drought, or do not have a very short life-cycle, do not survive on the most shallow soils.

Soil moisture affects both chemical and physical properties of soils. The availability of water in the soil affects plant growth and especially the capability to absorb nutrients needed for plant growth and development. Although nutrients in the upper soil layers represent important resources for plants (Grime et al., 1986; Robinson, 1994; Cui and Caldwell, 1997), these are the layers that undergo the largest fluctuations in moisture as well as temperature (Cui and Caldwell, 1997).

Chemical concentrations in soil solution are buffered to varying degrees against shifts in soil moisture by the exchangeable, precipitated, or adsorbed pools in the solid soil phase (Menzies and Bell, 1988; Wolt, 1994). By changing soil solution chemistry, moisture could regulate plant competition not only for available

water but also for nutrients, and influence the field distribution of plant species. Variation in soil moisture within ranges occurring in the field may greatly influence soil solution composition (Wolt, 1994). The concentration of mineral nutrients in the soil solution is an indicator of the mobility of nutrients both towards the root and in the soil (Marschner, 1995). Menendez et al. (1995) demonstrated a strong dependence of soil solution composition on soil water content. Increases in soil moisture content led to change in the ion distribution, free hydrated metal concentrations, and complexation (Fotovat et al., 1997). Soil chemical properties may exert a profound influence on growth and performance of plants (Grime and Curtis, 1976). By influencing root hair growth of plant, nutrient uptake efficiency may also be affected (Mackay and Barber, 1985).

The mechanisms of ion transport, nutrient supply and uptake by plants are influenced by water content of a soil. They are mainly based on interception, mass flow and diffusion (Dunham and Nye, 1976). Interception occurs as growing roots displace soil and the nutrients contained therein. This mechanism plays a minor role in nutrient supply, because roots occupy typically less than 1% of the soil volume, and the nutrient content of soil solution in that volume is usually insignificant compared to the total amount taken up (Smethurst, 2000). Mass flow is the transport of nutrients in soil water, as water moves towards a root due to plant transpiration. At typical rates of transpiration in moist soil, this mechanism supplies a significant proportion of nutrients that are present at high concentrations in soil solution or are almost exclusively in the solution phase, e.g. nitrate in most soils. If nutrient supply by mass flow is less than the rate of uptake, the concentration in solution at the root surface decreases. Nutrients will then diffuse down a concentration gradient towards the root. This mechanism of nutrient supply is particularly important for nutrients that are relatively immobile, e.g. phosphate in most soils. The relative importance of mass flow and diffusion depends on soil water content, the rate of uptake, the degree of

nutrient interaction with the solid phase, the concentrations of nutrients in solution, and nutrient demand by the plant. The importance of mass flow is minimal in dry soil.

Plants are often limited due to different environmental conditions. The field distribution of most south Scandinavian plant species is related to pH and other soil chemical factors (Tyler, 1993b; 1995; 1996b). Many conditions and chemical constituents of soils alone or in combination are known to limit growth and development of wild plants (Tyler, 1996b; 1996c). Some scientists (Inskeep and Bloom, 1984, 1986; Mengel et al., 1984; McCray and Matocha, 1992) have demonstrated that soil moisture has a great influence on soil chemistry of calcareous soil (high in CaCO_3 and with a high pH) by producing bicarbonate (HCO_3^-) which is supposed to be a main cause of chlorosis in many plants (Brand et al., 2000; Donner and Lyn, 1989; Russell, 1988; Coulombe et al., 1984). Phosphate and many micronutrients, such as Fe, Mn, Zn, and Cu, are quite sparingly soluble in high pH calcareous soils and might become plant growth limiting (Tyler, 1996b). Plants able to grow on this type of soil are called calcicoles.

Drying and rewetting of soil was reported to affect soil solution chemistry (Jones and Edwards, 1993). Such wet/dry fluctuations are common on alvar sites. The process of wetting and drying would be likely to enhance formation of less hydrated and more crystalline compounds of lower solubility, e.g., of Fe, Mn, Zn and Cu (Ryan and Hariq, 1983). Varying moisture content may cause significant changes in the extractability of microelements (Shuman, 1980). Calcareous soil already low in soluble Fe, Mn, Zn and Cu may eventually reach deficiency levels under such dry and wet conditions. Plants adapted to wet/dry conditions and able to utilize the solubility fluctuations may get advantage in

competition. Such cycles could, therefore, affect nutrient uptake, and influence the distribution of plants in the field.

Hypotheses and objectives

The main hypotheses are:

- (i) Soil moisture regime might influence soil solution chemistry and mineral nutrient concentration in native calcicole species.
- (ii) Soil moisture plays an important role in the distribution of plants. Calcicole species from dry habitats have relatively higher shoot nutrient content and biomass at low soil moisture compared to wet growing species.
- (iii) Wet/dry cycles in calcareous soil can influence nutrient availability and plant nutrient uptake.
- (iv) Plants able to utilise the solubility fluctuations are better competitors in nutrient poor soil under wet conditions, and vice a versa.

The objectives of my thesis are to illuminate and try to answer questions, originating from these hypotheses, applying greenhouse experiments under controlled conditions of soil moisture. Although thousands of published studies deal with manipulating water availability to plants, we still have a poor understanding of the influence of soil moisture on nutrient availability to wild plants, especially in nutrient poor soils.

Main findings

The studies presented in **papers I to IV** all concern the influence of soil moisture on soil solution chemistry and response of native calcicoles to differences and fluctuations in soil moisture. The experimental soil was always sampled from the Great alvar of Öland (56°25' N, 16°30' E), representing a Rendzic Leptosol according to the FAO-Unesco classification system. The plants used for experiments were either grown from native seeds of Öland or sampled from the same site.

Different but constant soil moisture levels (30%-100% WHC) of the water-holding capacity (WHC) were tested (**Papers I, II, IV**). Drying and wetting cycles, which are common on the Alvar, were also included in my studies to measure the response of plants to such conditions (**Paper III**).

Effect of moisture on soil solution concentration

Moisture exerts a considerable influence on soil solution chemistry, mineral uptake and tissue concentrations of plants on calcareous soil, which was demonstrated in **papers II and I**.

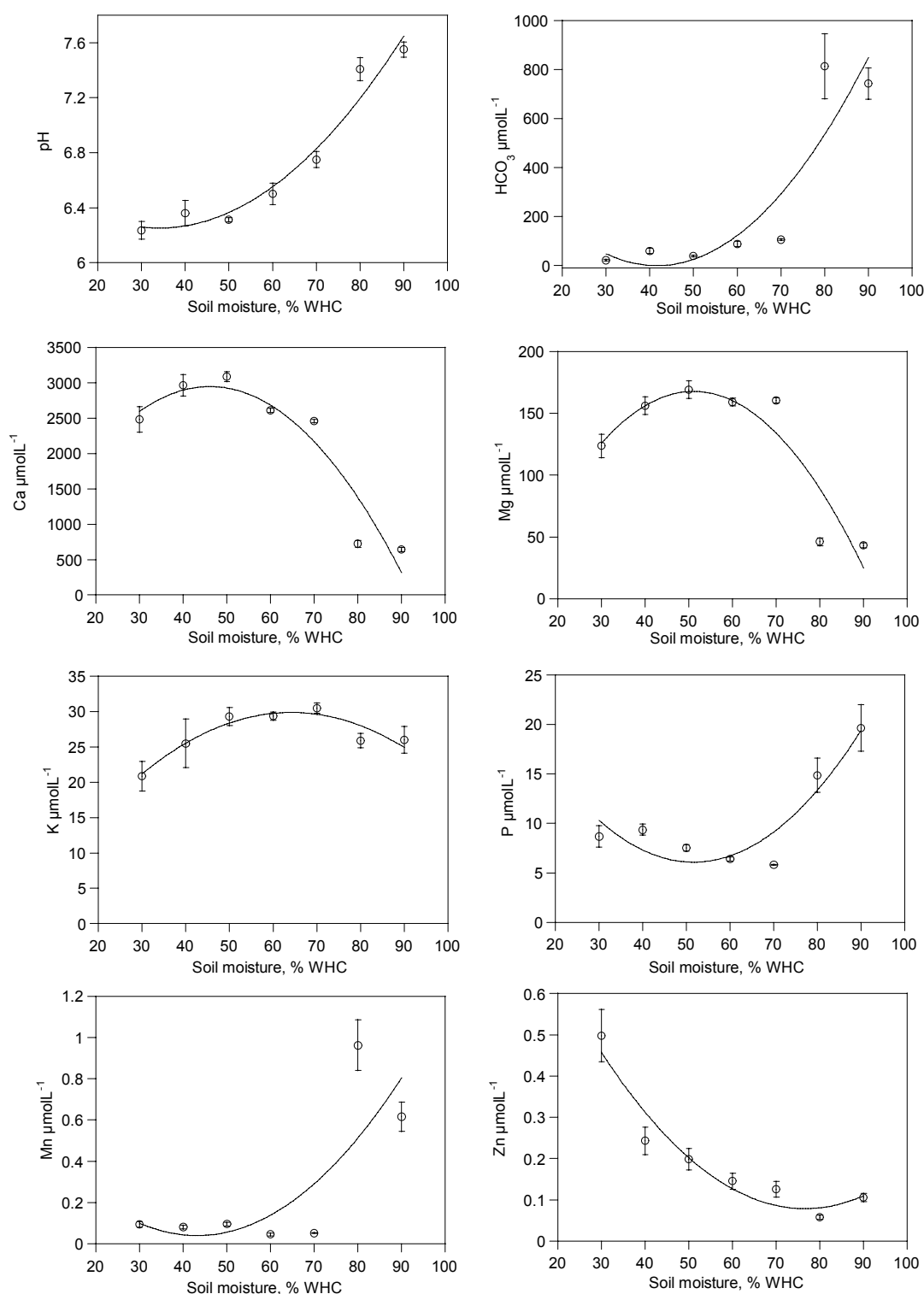


Figure 1. Second order regressions of soil moisture content on pH and on HCO_3^- , Ca, Mg, K, Mn, Zn and P concentrations ($\mu\text{mol l}^{-1}$) in soil solution. Means \pm S.E. (S.E. smaller than dot is invisible).

pH and bicarbonate

Increase of pH in soil solutions may play an important role in availability of those nutrients, which are pH dependent. The pH of soil solution was 6.2 at 30% WHC but increased to almost 7.6 at 90% WHC (Fig.1). A positive regression was obtained between soil moisture and HCO_3^- concentration, between soil moisture and pH, and between pH and HCO_3^- ($r = 0.912$) (**Paper I and II**). For HCO_3^- , most of the concentration increase occurred above 70% WHC. pH was negatively influenced when soil was subjected to wet/dry cycles. Significantly lower pH was observed under wet/dry cycles than at constant conditions (**Paper III**). Many investigations have shown that increase in soil moisture on calcareous soil could increase HCO_3^- and CO_2 in the soil solution (Inskeep and Bloom, 1986, Mengel et al., 1984, Ao et al., 1987, Yen et al., 1988, McCray and Matocha, 1992). Increase in HCO_3^- and pH on calcareous soil with increasing soil moisture could be due to the fact that when more water is added to the system, CO_2 (microbially produced) is less able to diffuse and escape from the soil, hence resulting in an increased partial pressure of CO_2 , displacing the carbonic acid equilibria in favour of HCO_3^- . Observed increase of HCO_3^- in calcareous soil with increasing soil moisture is not associated with ‘degassing’ of CO_2 as stated by Tyler (2000 a). Increase in HCO_3^- observed (**Paper I**) might be due to oxalate produced by microorganisms or from organic decomposition (Amrhein et al., 1993). Verrecchia and Dumont (1996) showed that bacteria transform oxalates into carbonates, and this might be an additional cause of increase in HCO_3^- as a result of increased bacterial activity. Change in soil pH due to increased HCO_3^- could alter the concentration of ions, which are pH dependent.

Calcium and magnesium

Calcium and Mg are not limiting on calcareous soil but high concentrations of these elements interact with other elements. In alkaline soils the Ca concentration of the soil solution is generally regulated by precipitation and dissolution of CaCO_3 . Lower Ca and Mg concentrations in soil solution at high soil moisture was observed in my study (Fig. 1), also reported by Bloom and Inskeep (1986) and Inskeep and Bloom (1986). These authors do not consider CaCO_3 dissolution in calcareous soils as a factor in determining HCO_3^- , which is obvious from the decrease in Ca concentration in my studies as well. Secondary calcite that precipitates from soil solutions enriched in soluble Mg often co-precipitates with MgCO_3 to form a magnesia calcite (Sposito, 1989). This can explain the decrease in Ca and Mg observed (Fig. 1). Vorob'yeva and Novykh (1986) calculated the solubility of calcite in alkaline soil and stated that at a given pH, the Ca concentration corresponding to the solubility of CaCO_3 decreases as the p_{CO_2} rises. Soil solutions might be highly oversaturated with the respect to the precipitation of calcite (Bloom and Inskeep, 1986).

Phosphorus

Phosphorus is a critical nutrient in semi-natural, unfertilised calcareous soils, usually limiting plant distribution and survival of plants (calcifuges) not adapted to such soils (Tyler, 1992; 1996a). Phosphorus is mainly soil water content dependent as diffusion is a dominating mechanism transporting phosphate ions to the root. (Dunham and Nye, 1976). Native inorganic phosphorus in calcareous soils is mainly present as an insoluble apatite like Ca phosphate. My study shows increase of P in the soil solution at high soil moisture which could be a result of increased pH (Fig. 1), as reported by Barber and Chen (1990). In high pH soils, dissolution of CaCO_3 controls the Ca level and may therefore increase

the solubility of P (Ao et al., 1987). Calcium phosphate is considered as a main source of phosphorus in calcareous soil and controls the solubility of phosphate; Ca phosphates are less soluble than Al phosphates if the soil pH is much higher than 6 (McBride, 1994), and Al phosphates are scanty in limestone soils. At pH 8, Ca phosphates are highly insoluble and the minute share of phosphate present in soil solution is mainly HPO_4^{2-} . A recent study done by Tyler (2002) on phosphorus fractions in grassland soils, however, indicates that easily exchangeable P fractions are mainly derived from the more labile forms of Al phosphate. It is possible that increase of P in soil solution with increasing soil moisture might mainly originate from released Al phosphate and not from Ca phosphate.

Zinc and manganese

Calcareous soils are often deficient in soluble Zn and easily available Mn. Exchangeable Zn is generally sorbed on soil surfaces as Zn^{2+} or ZnOH^+ . Zinc nutrition of plants in dry soils is often considered limiting due to low plant available concentration of Zn (Cakmak et al., 1996). Excessive rainfall (high soil moisture) may limit the supply of Zn and Mn to the plant roots due to dilution, and these elements do not readily return to their original levels in the saturated soil solution (Gammon, 1976). The concentration of Zn in the soil solution depends on factors such as concentrations of HCO_3^- and macronutrients. The decreased Zn concentration (Fig. 1) with increasing soil moisture observed might be the result of high HCO_3^- concentration, which can depress Zn availability by precipitation of franklinite-like solid material (Sajwan and Lindsay, 1986). Combination of high pH and CaCO_3 can also be considered major factors causing Zn deficiency (Cakmak et al., 1996). Solubility could also be controlled by interaction with phosphate and high pH, suppressing available and organic Zn (Tagwira et al., 1992). In calcareous soils, the diffusion

coefficient for Zn is about 50 times lower than in acid soils (Melton et al., 1973). Other antagonistic effects could be due to the increased solubility of P (Norvell et al., 1987; Tagwira et al., 1992).

Manganese is often considered a limiting element on calcareous soils. Manganese availability in soil is dependent on pH and redox reaction. The increase in Mn concentration followed the same pattern as HCO_3^- with increasing soil moisture; being closely correlated to HCO_3^- concentration ($r=0.955$) (**Paper I**). Soil moisture can influence the Mn status in soil. The sudden increase in Mn concentration of the soil solution at high soil moisture (Fig. 1) might be due to reduction of Mn (IV).

Other nutrients

Amounts of K and S in soil solution seem less influenced by soil moisture change (**Paper II**). There is often root competition for K uptake, which was not significant in **paper IV**. Concentrations of K in soil solution were highest at 50-70% WHC (Fig. 1) though differences were not great (Fig. 1). Diffusion rate of K is mainly controlled by supply of water to the soil but supply of K is also much dependent on soil fixation which often may occur during drying of soil (Barber, 1995). The author stated that CaSO_4 controls solubility of sulfate in soil solution. If the Ca level is 3 mmol/L, sulfate level will increase if Ca decreases. Ca concentration decreased at higher soil moisture (Fig. 1) but we did not find any significant result for S in soil solution related to Ca decrease with increasing soil moisture.

Decrease in shoot and root concentrations in *Phleum phleoides* at higher soil moisture above 68% WHC indicates that Fe was not available for plant uptake in the soil solution, as we did not find any significant influence of soil moisture on Fe concentration in soil solution (**Paper I**). It is also possible that decreased

availability of Fe might be indirectly influenced by soil moisture as a result of increased pH and HCO_3^- (Fig 1).

Response of plants to the changes influenced by soil moisture

Soil moisture in Rendzic Leptosols varies greatly, and this variability probably plays an important role in mineral nutrition of the vegetation of such soils, apart from the fact that calcicole plants have an inherent but greatly variable capacity to modify their rhizosphere.

Availability of nutrients in soil solution is important for all plants. Soil solution is the direct source of mineral nutrients to vascular plants; therefore knowledge about soil solution and fluxes of essential elements is of great importance in studying soil plant relationships and interactions (Tyler, 2000a). Soil-moisture induced changes in soil nutrient availability can affect plant distribution. Calcicoles that are adapted to grow on Ca rich soils are distributed in the field according to wet and dry conditions. Some calcicoles seem sensitive to moisture conditions and some are moisture stress tolerant. The distribution can be defined by the behaviour of calcicoles relative to soil moisture induced changes in the soil solution. I studied six calcicole species and their response to the changes induced by different soil moisture conditions.

Preferably dry growing species

Festuca ovina

Results indicate that *Festuca ovina* prefers constant but low soil moisture (**Paper III**). Concentrations of most elements in this species tended to be lower, though significantly lower in the plant biomass ($p < 0.05$) only for Fe and S under wet/dry treatment (Table 1). Higher concentrations of Mg and K in *F. ovina* soil

than *A. stolonifera* soil at the end of the experiment also indicates that *F. ovina* was less able to utilise these elements under wet/dry conditions (**Paper III**).

Table 1. Mean (\pm S.E.) shoot concentrations, and level of significance (p-values) of difference according to two-tailed paired t-test between means of the two treatments. Number of replicates of each species and treatment = 7. Concentrations given as $\mu\text{mol g}^{-1}$ dry weight.

	<i>A. stolonifera</i>			<i>F. ovina</i>		
	Wet /dry	Constant	significance	Wet / dry	Constant	significance
Ca	232.7(15.3)	212.8(10)	0.310	69.5(4.7)	75.1(2.6)	0.381
Cu	0.091(0.013)	0.164(0.021)	0.047	0.074(0.005)	0.084(0.004)	0.143
Fe	1.29(0.53)	2.27(0.38)	0.139	0.61(0.03)	0.96(0.10)	0.020
K	328.6(7.7)	369.7(13.5)	0.045	213.6(11.8)	221.8(9.5)	0.690
Mg	75.5(2.69)	82.5(2.00)	0.144	24.3(0.74)	27.8(2.0)	0.170
Mn	1.34(0.14)	2.19(0.09)	<0.001	0.47(0.06)	0.56(0.07)	0.204
P	18.1(0.7)	24.4 (1.7)	0.024	17.9(0.8)	17.4(0.7)	0.647
S	62.6(3.7)	86.4(4.2)	0.011	31.9(1.4)	38.5(1.6)	0.013
Zn	0.356(0.039)	0.592(0.035)	0.013	0.295(0.035)	0.353(0.019)	0.239

A decrease in Fe and K shoot concentration at higher soil moisture in *F. ovina* is consistent with field conditions (**Paper II**). Higher (relative to maximum) shoot production at low than at high moisture level in *F. ovina* than in *A. stolonifera* confirms the assumption that low soil moisture is less unfavourable to shoot growth for *F. ovina* (Table 2). The increase of Mn in soil solution at higher soil moisture (Fig. 1) could not be used by this species, as shoot concentration did not vary much with increased soil moisture (**Paper II**). This reflects the circumstance that *F. ovina* grows mainly on well-drained soil. Grime and Curtis (1976) considered the success of *F. ovina* in calcareous grassland to be due to its tolerance to low-moisture stress. Brar and Palazzo (1995) considered shorter plant canopy, slower growth, and low transpiration as drought avoidance mechanisms of *F. ovina*.

Table 2. Biomass (g dry wt. per pot) and relative shoot production (% of maximum) of *Agrostis stolonifera* and *Festuca ovina* at different levels of soil moisture. Means \pm S.E.

Moisture level	Agrostis stolonifera				Festuca ovina		
	WHC	Shoot	Root	Shoot % max	Shoot	Root	Shoot % max
30 %		0.143 ± 0.010	0.414 ±0.031	36	0.267 ± 0.047	0.272 ± 0.092	57
40 %		0.212 ± 0.025	0.542 ± 0.091	53	0.367 ± 0.084	0.406 ± 0.115	79
50%		0.244 ± 0.021	0.529 ± 0.076	61	0.342 ± 0.09	0.239 ± 0.04	74
60%		0.322 ± 0.025	0.582 ± 0.076	80	0.396 ± 0.028	0.277 ± 0.041	85
70 %		0.286 ± 0.043	0.439 ± 0.099	72	0.392 ± 0.039	0.339 ± 0.046	84
78 %		0.299 ± 0.026	0.515 ± 0.079	75	0.442 ± 0.080	0.282 ± 0.059	95
85 %		0.278 ± 0.019	0.369 ± 0.05	70	0.465 ± 0.039	0.774 ± 0.084	100
100 %		0.400 ± 0.034	1.075 ± 0.277	100	0.438 ± 0.052	0.650 ± 0.179	94

Melica ciliata

Melica ciliata is a tuft-forming grass on shallow soil, widely distributed in west central Europe with an isolated population in the south-central Baltic region. Its distribution is limited mainly by soil solution chemistry (Tyler, 1993a). Biomass production was increased with increase in soil moisture (**Paper IV**), despite of the fact that this is a species, which preferably grows under drained conditions. I tested the assumption that, being a dry growing species, *M. ciliata* might be a

better competitor at low soil moisture than the wet growing *Sesleria caerulea*. In mixed culture, there was no competition with *S. caerulea* for biomass production, but shoot concentrations of P was lower in monoculture compared to mixed cultures at 90% WHC. This shows that the demand of P in *M. ciliata* was comparatively less in monoculture than in mixed culture with *S. caerulea* (Table 3). Less demand of P in monocultures of *M. ciliata* may be related to a lower solubility of P ions at lower soil moisture (Fig 1), which is consistent with its field distribution.

Table 3. Shoot concentrations ($\mu\text{mol g}^{-1}$, means \pm S.E., n= 4). Letters (a, b, c) indicate differences of means between moisture treatments for mono and mixed culture per species, and significant ($p<0.05$) differences between mixed and monoculture for a specific treatment is indicated by (*).

	Fe	K	P	Mg
<i>M.ciliata</i>				
30%mono	2.39 ^a ± 0.56	378 ^{ab} ± 63	23 ^a ± 05	78 ^{ab} ± 17
30% mixed	2.09 ^a ± 0.14	288 ^a ± 46	24 ^a ± 01	84 ^{ab} ± 05
60% mono	2.39 ^a ± 0.27	527 ^{ab} ± 32	27 ^a ± 01	97 ^a ± 04
60% mixed	2.55 ^a ± 0.36	501 ^b ± 25	28 ^a ± 02	89 ^a ± 02
90% mono	2.50 ^a ± 0.32	541 ^{abc} ± 09	26 ^{*ab} ± 01	84 ^b ± 02
90% mixed	2.34 ^a ± 0.48	529 ^c ± 16	30 ^{*b} ± 02	82 ^b ± 03
<i>S.caerulea</i>				
30% mono	3.33 ^a ± 0.72	169 ^a ± 8	23 ^a ± 01	74 ^a ± 07
30% mixed	3.33 ^a ± 1.10	159 ^a ± 49	22 ^a ± 05	67 ^a ± 18
60% mono	3.32 ^a ± 0.43	254 ^b ± 30	34 ^a ± 04	91 ^{*a} ± 01
60% mixed	2.27 ^a ± 0.52	235 ^{ab} ± 06	30 ^{ab} ± 02	73 ^{*a} ± 03
90% mono	2.49 ^a ± 0.21	266 ^b ± 15	33 ^b ± 01	86 ^a ± 02
90% mixed	3.44 ^a ± 0.71	308 ^b ± 20	32 ^b ± 03	86 ^a ± 08

Veronica spicata

Nutrient concentrations were influenced by soil moisture in *Veronica spicata* (**Paper I**). *V. spicata* being sensitive above 70 %WHC showed decrease in total biomass (Fig. 2) which indicates that this species is sensitive to higher moisture. The shoot to root biomass ratio indicated a shift towards shoot biomass from 60% to 85% WHC in *V. spicata*. Calcium and Mg concentrations decreased in soil solution with increasing soil moisture (Fig. 1) but amounts and concentrations of Ca and Mg in *V. spicata* increased. Calcium and Mg are abundant in the experimental soil (**Paper I**) and these elements are therefore not limiting. Increase of these nutrients might be due to passive uptake. Increase in shoot and root biomass concentrations of P and Mn may be due to increased concentrations of these elements in soil solution (**Paper I**). Decrease in Zn amounts (**Paper II**) and concentrations could be explained by decrease in soil solution Zn at high soil moisture (Fig. 1).

Phleum phleoides

Greenhouse experiments results are only partly consistent with the field distribution of *Phleum phleoides* (**Paper I**). Total biomass was increased with increasing soil moisture (Fig 2). The shoot/root ratio of *P. phleoides* decreased with increasing soil moisture from 35% to 60% WHC, being lower at higher moisture levels. Opposite trends for Zn concentrations in roots and shoots of *P. phleoides* show that, with increasing soil moisture, relatively less Zn was transported to the shoots (**Paper I**). Amounts per pot of all elements in roots and shoots were influenced positively and linearly by the increasing biomass production with increasing soil moisture (**Paper I**). May be *P. phleoides* is more capable of controlling its uptake of mineral nutrients than *V. spicata*.

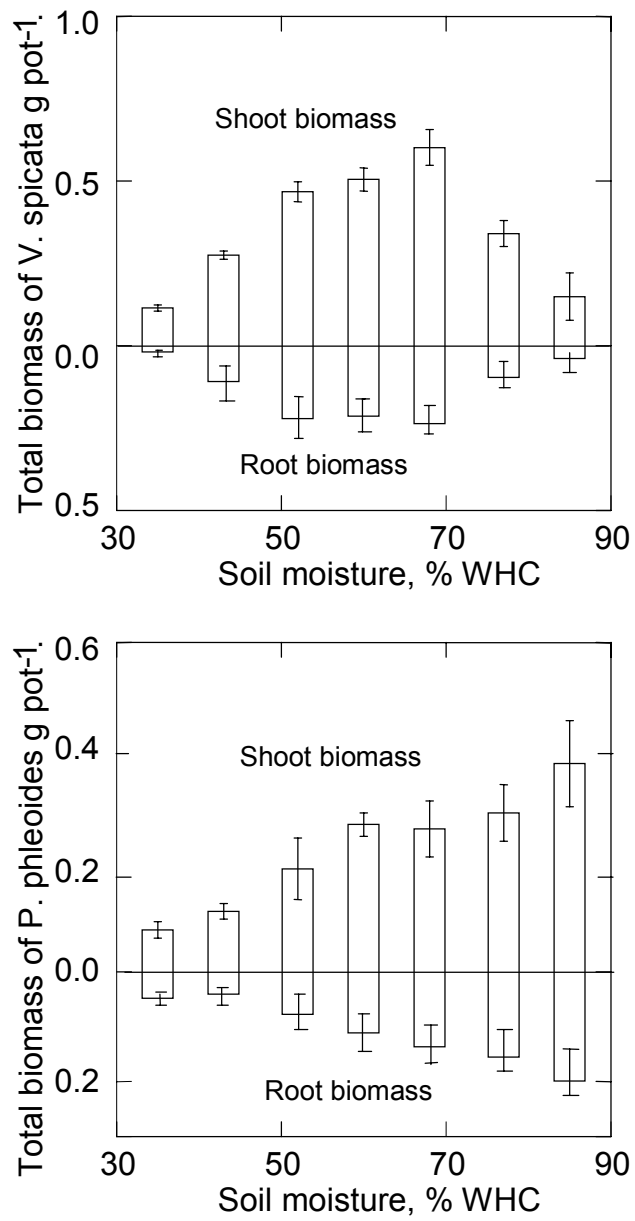


Figure 2. Shoot and root biomass produced (g dry wt. per pot) by *V. spicata* and *P. phleoides* at different soil moisture levels. Means \pm S.E.

Preferably wet growing species

Agrostis stolonifera

Agrostis stolonifera is a sword-forming grass of moist but periodically dry habitats in the Alvar, growing in and around shallow depressions flooded at least for some periods, particularly in the winter half of the year.

The positive correlations between shoot concentration and soil solution of *A. stolonifera* for amounts per pot of most elements indicate that uptake to a considerable degree is controlled by soil solution amounts, especially of Mn and Fe (Table 4). The more nutrients available in the soil solution, the higher were the amounts contained in the shoots.

Potassium concentrations in the shoots were relatively low at 30% WHC (**Paper II**), which may be due to the finding that K is less soluble at lower soil moisture (Fig 1). A sudden increase in Mn concentrations (**Paper II**), observed in shoots at high soil moisture, may be due to increase in soluble Mn under low redox potential at high % WHC (Fig 1).

Under wet/dry conditions shoot concentrations of Cu, K, Mn, P, S and Zn were lower ($p < 0.05$) than at constant water treatment. Concentrations of Fe and Mg also tended to be lower (Table 1).

Table 4. Linear and second order correlation coefficients between amounts (per pot) of elements in shoots and in soil solutions of *A.stolonifera*.

Elements	Linear r	2 nd order r
Ca	0.409**	0.408**
Mg	0.031	0.213
K	0.537***	0.566***
P	0.518***	0.521***
S	0.339*	0.593***
Mn	0.870***	0.952***
Zn	0.060	0.090
Fe	0.467**	0.713***

* p < 0.05, ** p < 0.01, *** p < 0.001.

Sesleria caerulea

Sesleria caerulea is a preferably wet growing species of calcareous soil. It was assumed that this species avoids drier soils in general and therefore might be a poorer competitor on nutrient poor soils under field conditions (**Paper IV**). Results from the greenhouse experiment indicated that the concentration of Mg at 60 % WHC was higher in monocultures than when grown with dry growing *M. ciliata* (Table 3). This might indicate that the demand of Mg was higher and this trait could be a disadvantage to this species in dry periods when comparatively less Mg is available, although this did not hold true when biomass production was considered. Increased concentration of Mg in monoculture at 60 % WHC also reveals that this species is more able to use increased solubility of Mg in soil solution at intermediate (50-60 % WHC) than

at lower (30-40%) soil moisture (Fig. 1), which agrees with its distribution in the field.

Discussion

Results indicate that amounts and concentrations of elements in soil solution and amounts in plants vary with soil moisture and that both similarities and differences are obvious in the variability of shoot nutrient concentrations between the species studied.

Results support the hypothesis that soil moisture has a profound effect on soil solution chemistry, directly by increased solubility of some ions (P and Mn) and maybe indirectly by increasing pH and HCO_3^- concentration, which may have an adverse affect on the solubility of Ca, Mg and Zn. A high positive correlation was measured between soil moisture and amount of HCO_3^- in soil solution as previously demonstrated (Inskeep and Bloom, 1984; Bloom and Inskeep, 1986; Ao et al., 1987; Yen et al., 1988; McCray and Matocha, 1992). This increase in pH and HCO_3^- can affect availability of some elements in the calcareous soil.

Most of the observed responses by the experimental species were highly correlated to soil nutrient availability conditions, as hypothesised. Availability of nutrients in calcareous soil is influenced by soil moisture (Fig. 1). It is of interest that concentrations of P and Mn, which are often considered limiting factors for some plants, increased significantly with increasing soil moisture. Under nutrient-poor conditions, many wild-growing plants may rather be favoured by some increase in the P status of the soil (Tyler, 2000 b; Theodose and Bowmen, 1997). Dry periods favour the solubility and availability of some nutrients to plants, wet periods favour others.

Some of the species from dry habitats were susceptible at high soil moisture. Decreased biomass production of *V. spicata* at high soil moisture indicated its susceptibility to high moisture regime (**Paper I**). Shoot concentrations of Fe, Zn and P were higher at low than at high soil moisture and this confirms my assumption that calcicoles from dry habitats have relatively higher shoot nutrient content at low soil moisture as hypothesised (**Paper II**). But this assumption was not confirmed in **papers IV and I**.

Soil moisture plays an important role in the distribution of plants. My results showed that the wet growing species respond better to the solubility of sparingly soluble elements of calcareous soil. Most of the wet growing experimental species were efficient in utilizing the increased solubility of P, Mn, and Fe. Occasional or transient wet conditions may be of great importance to the P, Mn, and Fe acquisition of some plants on normally dry calcareous soils. Increase in soil moisture can decrease the solubility of some elements like Ca, Mg and Zn. Decrease of the Zn concentration in soil solution due to increased moisture had adverse effect on the uptake of Zn in most of the species (**Paper I and II**). Soil solution concentration of Fe was less affected by moisture in my study and thus plants were not much affected. Species of well - drained soil can be sensitive to such conditions and when subjected to high soil moisture they can even develop chlorosis in some cases (**Paper I**).

Wet/dry cycles can influence nutrient availability and plant nutrient uptake. This was demonstrated in **paper III**. But **paper III** does not give any evidence that wet and dry cycles would be beneficial to biomass production and mineral nutrient acquisition of any of the species. There could be adverse effects of such a cycle on dry growing species. Lower shoot uptake of Mn in *F. ovina* with the wet/dry treatment suggests that greatly fluctuating soil moisture is unfavourable.

As hypothesised earlier, plant species able to utilise the solubility fluctuations can be better competitors in nutrient poor soils under wet conditions, or vice versa. Biomass production data provided no clue to confirm this hypothesis. Therefore, **paper IV** does not support the assumption that species from better-drained soils are poorer competitors than moist growing species. Regarding concentrations in biomass, I observed that *S. caerulea* had a lower shoot concentration of Mg at 60% WHC, when grown in mixed culture with *M. ciliata* than grown in monocultures (Table 3). It has been shown earlier (Ryser 1996) that under nutrient-poor conditions, species that initially grow fast will, in the long term, be competitively inferior to slow-growing species. Biomass production showed that *S. caerulea* is faster growing and produced comparatively higher biomass than *M. ciliata* in all treatments despite of the fact that *S. caerulea* prefers wetter soil. *M. ciliata*, being a slow growing species, might be P efficient due to a low demand of nutrient; this can be an adaptive trait. *M. ciliata* was more efficient in using P at 90% WHC, i.e., consumed less P (lower shoot concentration in monoculture compared to mixed culture) to produce an equal amount of biomass in monoculture than in mixed culture (Table 3). According to my results, the nutritional concentration in plants, as a competitive trait, seems to be more important than biomass production. This is in agreement with Koutroubas et. al. (2000). Furthermore Connie and Keddy (1988) stated that if biomass of two competitive plants is similar, then other factors might become more important in determining the outcome of the competitive interactions.

Decreasing concentrations of a mineral nutrient in the tissues of growing plants of well-drained soils indicate an inability of the plant to maintain the uptake rate of the nutrient but, on the other hand, may also show less demand of nutrients (**paper IV**). This could be of advantage for well-drained growing species that less demand of nutrients makes them more moisture-stress tolerant. Probably, in the

long run under field conditions, these species can compete better under long dry periods.

Main conclusions

Soil moisture in Rendzic Leptosols varies greatly, and this variability probably plays an important role in mineral nutrition of the vegetation of such soils, apart from the fact that plants have an inherent but greatly variable capacity to modify their rhizosphere.

The mineral nutrition limitations of calcareous soils are certainly to some extent also valid for calcicoles, not only for calcifuges trying to colonise such soils. The chemical changes in soil solution concentrations, created by soil moisture regime, could become both beneficial (increased Mn, P availability) and harmful (decreased Zn availability) to the nutrition of plants, depending on the demand of the species. Concentrations and amounts of P, Zn and Mn in most of the species were usually related to soil solution concentrations. These are elements with low solubility and availability in calcareous soils. In nutrient poor environments, dry growing plants which demand less nutrients, as observed in **paper IV**, might benefit in the competition during long dry periods, as P and Mn are less soluble at lower soil moisture (Fig. 1).

Soil moisture variability might even be a prerequisite for adequate mineral nutrient acquisition and growth of at least some plants on limestone soils. Manganese is not readily available to plants on limestone soils, and its concentrations in soil solution were found to increase with increasing soil moisture.

Originating from my studies I come to the following conclusions about difference and priorities of plants from wet and dry habitats. Plants which are mainly found on well-drained soils are generally slow-growing, demand less nutrients, have higher drought stress tolerance, and can probably take more advantage of adverse conditions of moisture in nutrient poor soil. They are less able to withstand high fluctuations of wet/dry periods.

Plants, which prefer moist soils, are generally fast-growing, nutrient uptake is high and they can withstand fluctuations of wet/dry periods. They are more able to utilize increased solubility of nutrients. Soil moisture variation may thereby influence the field distribution of native plants among habitats. Soil solution chemistry, as influenced by soil moisture regime, should be studied in order to increase the understanding of mechanisms of observed changes and differences.

It is true that nutrient uptake in plants depends on species demand and uptake efficiency, but solubility and availability of nutrients in soil solution is also important and much more dependent on soil water conditions.

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