Ecological aspects of a nutrient-deficient wet grassland

(Cirsio-Molinietum)

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Die niederländischen Pfeifengraswiesen (*Cirsio-Molinietum*) sind halbnatürliche, ungedüngte, artenreiche, nasse, einmal jährlich (im August) gemähte Wiesen auf (schwach) saurem, relativ nährstoffarmen Torf oder torfigen Sand; manchmal sind sie auch auf tonigem Torf oder Ton. Der Grundwasserstand reicht im Winter bis an die Bodenoberfläche; im Sommer können die oberen Bodenhorizonte für kurze Zeit austrocknen. Infolge der modernen landwirtschaftlichen Maßnahmen sind nur wenige Hektare dieses Graslandtyps übriggeblieben; sie stehen unter Naturschutz.

In der vorliegenden Arbeit wurde die Bedeutung des Mangels an verschiedenen Nährstoffen untersucht. Ein Düngeversuch mit ungestörten Rasenziegeln im Gewächshaus zeigte, daß das hohe Monokotyledonen/Dikotyledonen-Verhältnis nur dann bestehen bleibt, wenn weder Phosphat noch Nitrat gedüngt werden. Eine Zunahme der Bodenfruchtbarkeit ergab eine Zunahme der Produktion (standing crop), eine Abnahme der Artenzahl und eine Abnahme des Verhältnisses Monokotyledonen zu Dikotyledonen.

Keimversuche von frischen und kalt-stratifizierten Samen bei verschiedenen Temperaturen ergaben, daß alle untersuchten Arten keimen; jedoch bestehen beträchtliche Unterschiede in Keimbeginn und -rate sowie in der am Schluß erreichten prozentualen Gesamtkeimung.

Ein Topfexperiment mit Boden des natürlichen Standortes und vier ausgewählten Arten ergab, daß das Wachstum bei zunehmender Phosphatgabe gefördert wird, und zwar bei Agrostis canina stärker als bei Prunella vulgaris, Cirsium dissectum und Carex hostiana.

Es scheint, daß genügend tiefe Gehalte an Phosphat und Nitrat (was eng mit dem Grundwasserregime verknüpft ist) die wichtigsten Faktoren für die Erhaltung einer großen Artenzahl sind. Die artenabhängige Keimungsvariabilität scheint nur eine kleine Bedeutung zu haben.

Biomass production, botanical composition, dicotyledons, edaphic tolerance, fertilizers, germination, groundwater table, growth rate, management, marginal grassland, mineral nutrition, monocotyledons, vegetation structure.

1. Introduction

There is ample evidence from surveys of plant distribution in the field that certain plant species and groups of species are limited to certain types of soil (GRIME, HODGSON 1969). Where also records of nutrient contents were made, it appeared that soil nutritional factors can have a profound influence on the botanical composition. Best examples of soil effects on the distribution of plant species are plant communities growing on acidic, calcareous, serpentine and saline habitats.

Semi-natural grasslands at low levels of nutrients have in common that the species are slow-growing and are surviving towards the limit of their edaphic range. Their survival can be more related to tolerance of toxic polyvalent cations, imbalance of nutrients and various nutrient deficiencies than to high nutrient requirements. Low levels of nutrients allow two categories of species to survive: first an assembly of species with low nutrient requirements for growth; and second an assembly of species with a wide edaphic tolerance. The latter will usually grow far better in a fertile soil of intermediate pH.

Addition of major nutrients can lead to marked changes in the botanical composition of grassland (SONNEVELD et al. 1959; VRIES, KRUIJNE 1960; THURSTON 1969; DIRVEN, NEUTEBOOM 1975; BEHAEGHE, COTTENIE 1976; THURSTON et al. 1976). Increase of the nutrient status results in the gradual elimination of slow-growing species by an increased growth of species with a wide edaphic tolerance. These are in turn gradually ousted by a few highly competitive fast-growing species which are restricted to highly productive sites. The highest species diversity of permanent grassland is found at 5 to 6 tons standing crop plus litter per hectare annually (GRIME 1978, 1979, 1980; HUSTON 1979).

So far, for the sake of symplicity, floristic changes due to fertilizer application are considered against a background of otherwise constant management. But it has to bear in mind that the direction of vegetational succession is also controlled by factors such as the number of species present and their relative proportions, topography, management, etc. (KLAPP 1965; DIRVEN, NEUTEBOOM 1975; BAKKER 1978; BRADSHAW 1980; GREEN 1980; HAGGAR 1980).

Especially after World War II the production of permanent grassland in Western Europe has enormously increased by the application of chemical fertilizers but resulted also in impoverishment of the (local) flora. For a category of so-called 'marginal' grassland the costs of amelioration are frequently not benefited by the gain of production increase. Thereby, 10 000 of hectares of such grasslands are nowadays abandoned.

In the Netherlands these marginal grasslands are acquired to a large extent by the Government, and managed explicitly by once a year hay-making and omitting the addition of nutrients. This management imitates the kind performed in previous times and aimes the gradual decrease of nutrients. Mechanical management asks somewhat lower water tables than desirable for vegetational restoration. It is of primary ecological importance to know in which way it is possible to restore and maintain the original high biological diversity (LEEUWEN 1953). The fundamental question being asked is whether the already indicated relationship between soil nutrients and botanical compositon is completely reversible, not only taxonomically but primarily genetically.

In this scope I want to discuss some aspects of the nutritional ecology of 'Blauwgraslanden' ('Blue meadows') because these are probably the most nutrientdeficient wet permanent grasslands and are severely threatened (LEEUWEN 1953). Knowledge of their ecology would help us to manage them properly. 'Blauwgraslanden' are syntaxonomically classified as *Cirsio-Molinietum* Siss. et de Vries 1942, an association of the alliance *Junco* (*subuliflori*)-*Molinion* Westhoff all. nov. (WESTHOFF, DEN HELD 1969), and are man-manipulated, unfertilized, wet meadows with a rich flora. They are mowed once a year (in August) and grow on (weakly) acid, nutrient-poor peat or peaty sand; and sometimes on clayey peat or clay. In winter the groundwater table is very high and in many times inundation occurs for a few months. In summer the soil may dry out superficially for a short period only.

2. Materials and methods

A vegetation in the Dutch province of Friesland (near the village Veenhoop: Onlân fan Jelsma) was investigated. It is an area where in former times peat digging occurred intensively. This type of grassland is found growing on so-called lay-fields which means that the original type of soil profile was not man-disturbed.

From this habitat, the soil profile was described according to BAKKER & SCHELLING (1966); some soil characteristics were analysed and the fluctuation of the groundwater table during 12 months (1979-1980) was recorded. Soil samples were taken from the upper layer (O-10 cm), oven-dried and ground.

pH was measured in a soil suspension with a glass-Ag/AgCl electrode system; organic matter by weight loss on ignition at 950 °C and correction for carbonate; P by colorimetric molybdate (MURPHY, RILEY 1962) in extracts obtained by extraction of 1 volume of soil with 60 volumes of water (Pw-index; SISSINGH 1969), by extraction with ammonium lactate and acetic acid (P-Al-; HOFSTEE, FIEN 1971), and by digestion with perchloric-, nitric-, and sulphuric acid (P total); total N by a modified Kjeldahl technique (WEINIGER 1936); K and Ca by flame absorption photometry after extraction with hydrochloric- and oxalic acid (K) or sodium chloride (Ca); total Fe by digestion with 25% hydrochloric acid (HOFSTEE, FIEN 1971); and Al by extraction with potassium chloride and titration with hydrochloric acid via sodium fluoride (BLACK et al. 1965).

Short time changes in the relative proportions of the species present by the addition of major nutrients were established by using various nutrient solutions. In order to avoid the possibility of phosphate fixation, which is likely because the iron content of the soil is high, a double pot technique was employed in a heated greenhouse (min. temperature 17 $^{\circ}$ C) and long-day illumination (16 hours). This so-called Bouma-Janssen method consists of a combination of two pots (MULLER 1979).

The upper pot has a perforated bottom, and is filled with field-taken undisturbed turfs, so having the original balance of the species. The dimensions were 20 cm diameter and a depth of 10 cm. The lower pot is filled with demineralized water in the first stage of the experiment. When in the lower pots roots have penetrated through the bottom of the upper pot, the lower is filled with a nutrient solution up to 1 cm below the perforated bottom. The nutrient solutions were changed at regular intervals of 14 days, and all have an osmotic potential of -0.72 bar (30 mg ion./1) at 20 °C.

Compared were the effects of demineralized water throughout, a complete nutrient solution, and solutions lacking one specific macroion, and were randomly replicated 6 times. By doing so, it is possible to screen stepwise soil nutrient deficiencies. The turfs were clipped at intervals of 60 days, the samples sorted out, and dried at 70 $^{\circ}$ C for at least 12 hours.

From eight species present seeds were sampled during the vegetation period of 1979. After sampling they were air-dried at room temperature for a week, and immediately thereafter tested for their germination capacities at various constant and alternating temperatures. This imitates the situation just after seed shed. The tests were performed in petri dishes in which 50 seeds were spead on moist filter paper discs, replicated 3 times, and lasted 150 days ultimately. Germinated seeds were counted and discarded.

The effect of cold-stratification on subsequent germination at various temperatures was studied by storage of big numbers of seeds under moist conditions at 4 $^{\rm O}$ C for 100 days.

The soil was bio-assayed for P status by studying the growth of seedlings of four species (*Carex* hostiana, *Cirsium dissectum*, *Prunella vulgaris*, and *Agrostis canina*). The species chosen cover the differential individual response to nutrients as established by the double pot experiment.

Seedlings were germinated as described before and transferred to plastic pots as soon as the coats investing the seed were shed. Seedlings were grown on the soil in pots at 3 seedlings per pot with four replicate pots per treatmant. The pots were randomized in a growth room, which provided a day length of 14 hours and a light intensity of 6500 lux by cool white TL 33 tubes at plant height. The day temperature was 23 ± 2 °C, the night temperature was 15 ± 2 °C. Relative humidity fluctuated opposited to temperature between 70% and 90%.

Pots (16 cm diameter) were filled with 1350 g of thoroughly mixed soil (moisture content 57.7%) of which most of the roots were sorted out. The soil was initially supplied with adequate amounts of macroions (exept P) and trace elements. P supply (as $Ca(H_2PO_4)_2 \cdot H_2O$) was varied in amounts yielding a range up to 39.1 ppm P. Watering was carried out daily using demineralized water.

After a fortnight two out of three seedlings per pot were discarded following visual judgement for uniformity. The plants were harvested after two months of growth, dried at 70 $^{\circ}$ C for at least 12 hours and weighed.

3. Results

depth (cm)

3.1 Description of the site

The site investigated is dominated by phanerogams such as Carex hostiana, C. panicea, C. x fulva, Molinia caerulea, Sieglingia decumbens, Nardus stricta, Anthoxanthum odoratum, Agrostis canina, Cirsium dissectum, Succisa pratensis, Plantago lanceolata, and Prunella vulgaris. The nomenclature is that of HEUKELS & OOSTSTROOM (1977).

The soil profile (Table 1) can be described as a prominent clayey earthened moss peat soil, consisting of different well-marked layers. The upper two layers are clay; the lower ones are peat.

Table 1: Profile description of prominent clayey earthened moss peat soil, and some analytical data of the upper layer (0-10 cm) which corresponds roughly with the depth of rooting of a Blue meadow vegetation (Cirsio-Molinietum).

•			рН ₂ О	4.6	
0	Al g	mucky,silty clay	pH Kcl	4.0	
-8			organic matter	29.2	%
	C1 g	humus poor, heavy	Pw-index	3.3	Υ P ₂ 0 ₅ /cc*
-20		clay	p-Al-	1.8	mg $P_2 O_5 / 100 g^{**}$
	01	oxidized, dark-	P total	160	mg $P_2 O_5 / 100 g^{**}$
			N total	0.9	%
		brown mood pour	K exchangeable	17.7	mg/100 g ^{**}
			Ca exchangeable	174	mg/100 g ^{**}
-60			Fe total	2436	mg/100 g ^{**}
	non-oxidized.reddish-	Al exchangeable	88.9	mg/100 g ^{**}	
	02	brown moss peat, and light-brown sedge peat	★ 35 [°] C - ★★ 100 [°] C -	dry soil dry soil	

3.2 Soil analysis

The results of a soil analysis of the rooted depth is also given in Table 1. It indicates at least a low pH, a very low P availability, a low total N content as well as low exchangeable K. On the contrary, the Fe- and Al contents are high.

3.3 Fluctuation of the groundwater table

The fluctuation of the groundwater table is shown in Fig 1. The groundwater table in summer seems to be low, presumably too low as compared to other Blue meadow sites.



Fig. 1: Fluctuation of the groundwater table of a Blue meadow vegetation during a 12 months period. The amount-duration-frequency groundwater line is included.

3.4 Effect of various nutrient solutions on growth

The technique used and some of the qualitative results are shown in Fig 2. The upper part demonstrates the technique, the middle part the effect of macroanion-deficient nutrient solutions, and the lower part the effect of macrocation-deficient solutions. The right pot shows the effect of the complete nutrient solution, and the left one the effect of demineralized water throughout.

Fig. 3 shows that plant biomass is greatly increased of a complete nutrient solution is used, or those lacking magnesium or sulphate. If, however, the nutrient solution is deficient in K, plant biomass is partly increased but probably only during the first stage of the experiment. Later on, plant biomass stimulation decreases. For nutrient solutions lacking Ca, more or less the same trend is observed. The primary cause seems not to be Ca deficiency of the tested soil, but inadequate root growth in the lower pot. Nutrient solutions lacking P or N affect plant biomass severely in such a way that plant biomass stimulation is very small. In the last part of the experiment it is found that the overall plant biomass decreases no matter the treatment.

The effect of the various nutrient solutions on the growth of both monocotyledons and herbs is presented in Fig 4. If plant biomass is stimulated, it is mostly due to growth stimulation of the herbs. Nutrient solutions deficient in P or N exert some growth stimulation of the monocotyledons, while those of the herbs is not affected. When Ca or K is omitted, growth of the dicotyledons is only affected.

Changes in the relative proportions of the species by the supply of various solutions is given in Fig 5. The original high monocotyledons/dicotyledons ratio is only maintained if N or P supply is omitted. In the case of omitting K supply this ratio decreases. This decrease, however, is smaller as compared to the decrease caused by the addition of, for example, a complete solution.

So far, the effects of various nutrient solutions on plant biomass, and on the monocotyledons/dicotyledons ratio are compared. Looking at the effect on the growth reaction of some individual plant species, two kinds of reactions are observed. In Fig. 6 is illustrated, as shown by *Carex* spec., that monocotyledons such as *Nardus stricta*, *Sieglingia decumbens*, and *Molinia caerulea* are negatively affected if a complete nutrient solution or a nutrient solution deficient in Mg or S is added. On the other hand, the growth of some monocotyledons is stimulated. This



Fig. 2: Qualitative view of the stepwise screening of Blue meadow turfs for relative nutrient deficiencies by the Bouma-Janssen double pot method.

(A) shows the housing of the pots in the greenhouse;
(B) and (C) show the effects of anion- and cation-deficient nutrient solutions, respectively, as compared to the effects of demineralized water and complete nutrient solution.

is indicated by Anthoxanthum odoratum. Species belonging to this group are Agrostis canina and Holcus lanatus. Growth of dicotyledons is always increased by N, P and K supply which is represented by the growth reaction of Cirsium dissectum.

Omitting K results in a decrease of growth stimulation later on. Especially the dicotyledons (Fig. 5) are affected as such, which is exemplified by *Cirsium dissectum* (Fig. 6). K deficiency became visible by necrotic spots on the leaves.



a date of harvest in 1979

Fig. 3: Effect of adding various nutrient solutions to turfs of a Blue meadow vegetation on plant biomass (g dry matter/pot). Specific deficient solutions are indicated by the macroion as such (A): macro-anion deficient solutions; (B): macro-cation deficient solutions.



66¹⁰/08⁹/10¹⁰/12 date of harvest in 1979

Fig. 4: Effect of adding various nutrient solutions to turfs of a Blue meadow vegetation on plant biomass (g dry matter/pot) of monocotyledons and dicotyledons. Specific deficient solutions are indicated by the macroion as such. (A), (C): macro-anion deficient solutions; (B), (D): macro-cation deficient

3.5 Temperature affected germination

solutions.

In Fig. 7 is shown that fresh seeds of three *Carex* species are capable of germinating. It seems that constant temperatures are not very suitable. At alternating temperatures germination is greatly favoured. If the seeds are stratified as indicated, seeds germinate freely, especially at alternating temperatures. This seems not to apply to *Carex panicea*. There is a tendency that germination is stimulated when the temperature rises (*Carex panicea* and *D. demissa*). *C. hostiana*, however, germinates optimally at 20 °C or at 25/15 °C. Generally, these species germinate very slowly.



Fig. 5: Effect of adding various nutrient solutions to turfs of a Blue meadow vegetation on the monocotyledons/dicotyledons ratio (%) For further details see caption under Fig. 3.

Fresh seeds of *Holcus lanatus* germinate freely at constant and alternating temperatures. At constant temperatures, 10 °C is better than higher temperatures. Stratification was not successful since within few weeks most of the seeds had already germinated.

The four dicotyledons examined germinate as indicated in Fig. 8. It is found that germination of fresh seeds increases if the temperature rises (*Cirsium dissectum*, *Plantago lanceolata*, *Prunella vulgaris*). Again, alternating temperatures are more responsive than constant temperatures. If the seeds are stratified, they are able to germinate even at relative low temperatures. On the contrary, germination of *Centaurea pratensis* deviates somewhat from this general pattern.

3.6 P affected growth

Since it was found that, among other things, P supply greatly dominates the relative proportions of the species present, it is thought that individual species will react differently if P addition is varied against a background of otherwise constant basic dressing of the original soil. The results are given in Fig. 9. It may be seen that the slow-growing *Carex hostiana* is somewhat stimulated if P supply increases. *Cirsium dissectum* may grow vigorously (Fig. 6), but the growth is now not severely stimulated. A species with a moderate edaphic tolerance such as *Prunella vulgaris* is somewhat more responsive. The highest growth stimulation is found for *Agrostis canina*.

4. Discussion

The soil profile of the investigated site can be described as a prominent clayey earthened peat moss. The descriptive characteristics closely resemble those as established by CNOSSEN (1971). It appeared from correlative field studies that this type of wet grasslands occurs on soil of poor fertility which would be characterized by low levels of P, N, and K (LEEUWEN 1953).

Records made of soil nutrient contents and distribution of plant species revealed that almost all of the species present indicate low levels of nitrogen (ELLENBERG 1979), and low levels of phosphate and potassium (KRUIJNE et al. 1967). Analysis of the rooted depth of the soil made plausible that the levels of P, N, and K are low, despite the lack of information concerning spatial and seasonal nutrient content variation. The figures found agree with those given by CNOSSEN (1971).



Fig. 6: Effect of adding various nutrient solutions to turfs of a Blue meadow vegetation on growth (% dry matter/pot) of Carex hostiana and C. panicea, Anthoxanthum odoratum, and Cirsium dissectum For further details see caption under Fig. 3

Bio-assaying of the soil with undisturbed turfs for nutrient-deficiencies showed that the soil is indeed deficient in P, N, and partly K. Whether or not Ca supply is sufficient, is uncertain. Mg and S supply seem to be adequate. The dominant role of P deficiency is obvious. It is therefore predictable that regular fertilizer application of P, N, K, and Ca will ultimately result into a drastic change in species composition, and increase of the annual production (KLAPP 1965).

The technique employed has the advantage, that changes in relative proportions of the species present following nutrient addition, can be assessed relatively rapidly. It assumes that all the species possess the same capacity to form new roots in the nutrient solution. The disadvantage is that dissemination from elsewhere is excluded. The period of utility is restricted due to the limited volume of soil being assayed. Nevertheless, the results obtained in this way are highly consistent with field observations which are chiefly based on spatial comparisons.

Such experiments have the advantage of ensuring that the response measured is (partly) ecologically real, operating in the original setting of the individuals of the species present, but is ineffective in connecting cause and effects; an unavoidable characteristic when nature and extent of competition are unknown.



Fig. 7: Effect of various constant (●, o), and alternating (▲, △) temperatures on germination (final %) of freshly-collected (closed symbols) and cold-stratified (open symbols) seeds. Species examined: Carex hostiana, C. panicea, C. demissa, and Holcus lanatus.



Fig. 8: Effect of various constant (●, 0), and alternating (▲, △) temperatures on germination (final %) of freshly-collected (closed symbols) and cold-stratified (open symbols) seeds. Species examined: Cirsium dissectum, Plantago lanceolata, Prunella vulgaris and Centaurea pratensis.

To link nutrient addition and response, results under more or less controlled conditions are needed for supplemental evidence. Such a study as has been made with four selected species (Carex hostiana, Cirsium dissectum, Prunella vulgaris, and Agrostis canina) based on this simple response hypothesis, tends to confirm this assumption. These results closely resemble those of BRADSHAW et al. (1960) on the growth of several grass species at various levels of P in solution. It is found in the present study that a species such as Agrostis canina responds to the range from 6.3 to 39.1 ppm P, while at the other extreme Carex hostiana is much less responsive. BRADSHAW et al. (1960) found that a species of fertile habitats such as Lolium perenne responds to the whole range from 5 to 125 ppm P, while Nardus stricta, a plant species of infertile habitats, shows no response at all. Nardus stricta actually shows a decline in yield at increased soil fertility.



Fig. 9: Effect of various P additions to Blue meadow on growth (g dry matter/pot) of seedlings of Carex hostiana, Cirsium dissectum, Prunella vulgaris and Agrostis canina.

Such differences accord with the habitat preferences of three Agrostis species (CLARKSON 1967). At low rates of P supply, A. canina was slowed by P deficiency, whereas A. setacea, a plant species of acid, nutrient-poor heaths, maintained exponential growth. RORISON (1968) found that four species from very different habitats had comparable differences in their growth response to phosphate.

Notwithstanding the fact that almost all of the species present point to poor soil fertility, some species, such as Agrostis canina, Anthoxanthum odoratum, Plantago lanceolata, and Cirsium dissectum are favoured when soil fertility is increased. Such a rather strong phenotypic plasticity is related to a wide edaphic tolerance. This characteristic was unexpected as far as Cirsium dissectum is concerned. Due to increased competition by nutritional growth stimulating, the less- or non-responsive species will be ousted.

It is clear that the original high monocotyledons/dicotyledons ratio is only maintained when soil fertility is low. The P-status of the soil seems to play a decisive role. However, when the groundwater table is lowered too much in summer, the species composition will change (GROOTJANS et al. 1979) by increased N supply as a result of increased mineralization, and by invasion of drought-adapted species The occurrence of species such as *Nardus stricta* and *Festuca ovina*, both of infertile but dryer habitats, may endorse the view that hydrology of the investigated site must have changed temporarily in the past.

The species examined thusfar are able to germinate at normal temperatures, even immediately after dissemination. This points to the absence of true dormancy of the seeds. The highest germination percentages are most commonly found at relatively high temperature. At constant as well as at alternating temperatures the proportion of seeds that germinate tends to increase with rising temperature up to an optimum, and very likely decreases at still higher temperatures. The rate of germination follows the same pattern, but the optima frequently occur at slightly different temperatures (GULLIVER, HEYDECKER 1973). As found many times (LANG 1965), alternating temperatures are more beneficial. The cause is not quite understood.

The function of this type of partial dormancy is comparable to true dormancy: it determines the timing of growth resumption whenever external conditions become suitable. The timing is enforced by the effect of stratification (VEGIS 1964; LANG 1965; VEGIS 1973). Such a germination pattern is typical of species adapted to a climate with a periodically recurring cold season, although not all the species follow this (grasses such as *Holcus lanatus*; fig. 8).

Seedlings are being encountered during the whole year, very likely due to the open structure of the vegetation. The numbers, however, fluctuate: the smallest

 $_{\rm n}{\rm umbers}$ are metin summer. Because many of the seedlings do not establish themselves, the rate of turnover seems to be low.

When occasionally gaps are created, especially seedlings of Carex demissa, Ranunculus flammula, and Agrostis canina are abundant at first. Somewhat later seedlings of Carex hostiana, C. panicea, and Cirsium dissectum are seen. Whether they are recruited from a persistent seedbank is not known. These qualitative observations demonstrate that the number of species and their relative proportions in gaps strongly deviate from those observed in the established sward. It seems likely that it will take some years in which the original situation is restored. A species which is particularly abundant in open places is Carex demissa. In the closed sward it occurs occasionally. Germination characteristics, therefore, do presumably not account for the distinct species composition. It would appear that selection occurs later in the life cycle.

The major conclusion which may be drawn is that it is of primary importance for maintaining this type of wet grasslands a sufficiently low level of at least phosphate and nitrogen, combined with a relatively high groundwater table in summer.

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