

Ranunculus hederaceus L. as indicator of land use changes in The Netherlands

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SUMMARY

In The Netherlands *Ranunculus hederaceus* is a rare species that occurs in running waters. It appears to be confined to zones with a constant supply of mineral-poor groundwater, originating from highly fertilized fields.

The relation between species performance and chemical composition of the water was investigated by means of response analysis. No relation was found unless the mineral content of the water was multiplied with stream velocity (yielding a measure for mineral supply per time unit). In the latter case significant correlations were found for calcium, bicarbonate, sodium, chloride and sulphate.

We discuss whether low P-availability in the system could limit biomass production of *Ranunculus hederaceus*, although this appeared to be unlikely. Competition for light with algae and large helophytes is more likely to be a major reason for the absence of the species in stagnant waters.

The situation near Oudemolen illustrates the indicative value of the species. Detailed investigations showed that artificial drainage changed the original mesotrophic conditions into eutrophic circumstances, which are much more favourable for this species. Hence, the increase of a rare plant species like *Ranunculus hederaceus* does not always indicate the well-being of a nature reserve.

Key-words: hydrological relations, macro-gradient; response analysis, water chemistry.

INTRODUCTION

Aquatic macrophytes have been used for the assessment of environmental factors, both in stagnant (Wiegand 1978; Pott 1983; Bloemendaal & Roelofs 1988) and in running waters (Kohler *et al.* 1973; Wiegand 1981; 1984; Carbiener *et al.* 1990). Bio-indicators are assumed to integrate seasonal variations in water quality parameters, which can

Nomenclature: Van der Meijden (1990) for phanerogams, Westhoff & Den Held (1969) for syntaxa, and Hooghart (1986) for hydrological terms.

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otherwise be revealed only by a very intensive hydrochemical sampling programme (Carbiener *et al.* 1990). An ideal bio-indicator has a narrow range with respect to the factor(s) it is to indicate, it responds quickly to changes in the environmental conditions, and it is easily recognizable. The macrophyte *Ranunculus hederaceus* could be such an ideal indicator of the chemical composition of the surface water. In The Netherlands the species grows in ditches with running water, from which the vegetation is removed each year in autumn. It has a weakly developed root system, which suggests that the absorption of minerals occurs mainly in the leaves (Denny 1972). As *Ranunculus hederaceus* has to re-establish itself every year, a delayed response to environmental changes, as in some perennial species, is unlikely (Ernst & Van der Ham 1988; Van Diggelen *et al.* 1991). Moreover, the species can easily be recognized, even vegetatively.

Early phytosociologists considered the species to be indicative of slow-flowing, clear water, poor in calcium and nutrients (Libbert 1940; Tüxen & Jahns 1962). Later studies (Cook 1966; Segal 1966; Ludwig 1970; De Sloover *et al.* 1977) showed that the species could also be found under eutrophic conditions. Consequently, it can be encountered in a broad range of plant communities from the spring community *Cardamino-Montion* (Tüxen & Jahns 1962; Oberdorfer 1990; Runge 1990) and the water plant community *Callitricho-Batrachion* (Den Hartog & Segal 1964; Westhoff & Den Held 1969) to terrestrial communities like *Nanocyperion flavescentis* and *Bidention tripartitae* (De Sloover *et al.* 1977). These findings suggest that the ecological range of the species is quite large. One could easily be tempted to believe that it could occur everywhere. Yet it is rare in most of its distribution area (Ludwig 1970; Delvosalle *et al.* 1970; Nilsson & Gustafsson 1976; Mennema *et al.* 1985; Haeupler & Schönfelder 1988; Weeda *et al.* 1990).

In a previous study (Van Diggelen & Klooker 1990) the distribution of *Ranunculus hederaceus* in The Netherlands was investigated in relation to water flow systems. Its current distribution appeared to be confined to stable hydrological gradients, assumed to have a constant supply of poorly mineralized ('soft') groundwater. The decline of the species in several parts of The Netherlands coincided with changes in land use in the surrounding areas.

The present study aimed at investigating these relations in more detail. First we analysed the hydrological relations between the habitats of *Ranunculus hederaceus* and the surrounding landscape to check if the gradients are indeed as stable and the water as mineral-poor as assumed. We studied these gradients in a few sites that differed in hydrologically relevant conditions: (i) soil type; (ii) geohydrology; (iii) management of the adjoining grounds. To understand why *Ranunculus hederaceus* is restricted to these types of gradients we then measured the direct relation between the performance of the species and the hydrochemical characteristics of its habitat. The results we found were used to shed light on the question of why the abundance of *Ranunculus hederaceus* changes after changes in the land use of the surrounding grounds.

METHODS

Hydrological relations between Ranunculus hederaceus habitats and the surrounding landscape

Study areas. The hydrological relations of three *Ranunculus hederaceus* stands with the surrounding grounds were investigated in three study areas in the northern part of The Netherlands: Deurze, Gieten and Oudemolen.

The area Deurze (52°59'N, 6°37'E) lies in a small valley along a tributary of the Drentse Aa river. The soil is of a humus-rich sandy type and the area is agriculturally used. At a depth of about 20 m an impermeable Elsterien clay layer of some 50 m thickness prevents a connection between the shallow groundwater system and deeper aquifers (WRGOD 1978). The whole area is covered with intensively used arable fields, with the exception of the valley where fertilized meadows are found. *Ranunculus hederaceus* occurs here in two ditches with running water.

The study area Gieten (53°01'N, 6°47'E) is located at the bottom end of an altitude gradient between the 'Hondsrug', an ice-pushed moraine ridge at 15–20 m above mean sea level (a.m.s.l.), and the valley of the river Hunze (2 m a.m.s.l.). Impermeable layers are absent to a depth of at least 150 m and groundwater from deep aquifers discharges in large quantities in the river valley (WRGOD 1978). The soil of the 'Hondsrug' and its flanks is of the podzolic type, whereas a humus-rich sandy soil is present in the valley.

The top of the 'Hondsrug' has been partly planted with pine and is otherwise covered with intensively used arable fields. Drainage ditches were dug from the valley flanks to the river Hunze. All these ditches contain running water and *Ranunculus hederaceus* is found in several of them.

The study area Oudemolen (53°03'N, 6°39'E) is part of the stream valley reserve 'Drentse Aa' (Bakker 1989). Geological investigations show medium fine and fine sand layers to a depth of more than 50 m, while thin clay layers are locally found near the surface (WRGOD 1978; Grootjans *et al.* 1987). The soil is sandy along the valley flanks, while a convex shaped peat body of up to 4.5 m in the centre of the valley is witness to the considerable groundwater discharge in former days. There is still a difference in water pressure of about 1 m between groundwater at 4 m depth and the phreatic water (Grootjans *et al.* 1987), but this water is nowadays diverted into ditches and can no longer reach the rootzone (Bakker & Grootjans 1991). Nutrient-rich water from the flanks can now enter the valley to a considerable extent.

The valley flanks are covered by fertilized meadows while the valley itself is a nature reserve. The latter is covered mainly by meadow communities, belonging to the alliance *Calthion palustris*. Locally tall herb communities (*Filipendulion ulmariae*) occur (Bakker & Grootjans 1991). *Ranunculus hederaceus* was found for the first time in 1974. It has increased ever since and nowadays is present in most of the ditches in this part of the reserve.

Description of the hydrology. The hydrology was described in each study area along a transect of 50–150 m length, chosen in such a way that it comprised the whole zone in which *Ranunculus hederaceus* was found. Each transect consisted of 5–6 locations where piezometers were installed with filters at three different depths (15, 45 and 70 cm below soil surface).

The chemical composition of surface water and phreatic water along these transects was measured three times (21 March 1989, 24 April 1989, 4 July 1989). To be sure that fresh groundwater was taken, the piezometers were emptied 1 day before sampling. Electric conductivity at 25°C (EC₂₅), temperature and pH were measured directly in the field, while Ca²⁺, Mg²⁺, Na⁺, K⁺, HCO₃⁻, Cl⁻, SO₄²⁻, NO₃⁻, NH₄⁺ and P₂O₅ were measured in the laboratory, using standard techniques (see Van Diggelen *et al.* 1991). To check the reliability of the analyses, both the charge balance and EC₂₅ were computed. Unreliable analyses (a deviation in the charge balance of more than 10% from electroneutrality of a difference in computed vs. measured EC₂₅ of more than 15%) were

discarded. We computed the similarity (cf. Van Wirdum 1991) between the chemical composition of each water sample to Van Wirdums 'standard water types' (atmospheric rainwater, lithotrophic groundwater and thalassotrophic sea water) for a clue to its origin.

Differences in hydraulic head between surface water level and groundwater level were measured to identify discharge and recharge zones. We combined these results with the hydrochemical data and available hydrogeological information into a 'hydro-ecological model' (cf. Everts *et al.* 1988), which shows the influences of various ground and surface water flows along the gradient. This procedure was repeated for each sampling date to check if substantial shifts in the importance of different water flows had occurred.

Species performance in relation to habitat characteristics

Sampling sites. The relation between the chemical environment and the abundance of *Ranunculus hederaceus* was investigated in a number of populations, where the species is known to have been existing for at least a decade. Data were collected in the areas selected for the case studies (Deurze, Gieten, Oudemolen) and four other areas. The latter sites were found along the inner edge of the coastal area near Schoorl (52°42'N, 4°41'E), in the transition zone between the pleistocene sandy hills and the neighbouring holocene polder area near Soest (52°11'N, 5°19'E), and in the end moraine landscapes near Ootmarssum (52°26'N, 6°53'E) and Havelte (52°47'N, 6°19'E).

Data collection. 31 samples of the surface water were taken and stream velocity and water depth measured in the beginning of spring when the growth rate—and thus the nutrient demand—was assumed to be maximal. Two months later, when the vegetation cover was maximal, relevés were made using the decimal scale of Londo (1976). They covered a surface of 2–4 m².

Data-analysis. A first impression of the ecological tolerance of *Ranunculus hederaceus* with respect to the chemical composition of the surface water was achieved by statistically evaluating the collected data. Mean values were compared to ecological fresh water quality standards in The Netherlands (CUVWO 1986). The water samples were then classified according to limits given by Bloemendaal & Roelofs (1988) to check whether N- and/or P-limitation was apparent.

The next step was to investigate whether the performance of *Ranunculus hederaceus* indicated environmental parameters more accurately than the mere presence of the species. Correlations between performance (expressed as cover degree) and chemical composition of the surface water were determined by univariate response techniques. The computer program NLR ('Non Linear Regression'), available in the program package SPSS PC (Norusis 1990) was used for this purpose. The analysis started with a simple model, describing an increasing or decreasing trend, and subsequently proceeded to more complex ones. The procedure stopped either when a more complex model could not explain significantly more of the observed variation than the previous step or when the most complex model, a skewed unimodal response curve, was reached. A more detailed description of this technique is given in Huisman *et al.* (1993).

We also investigated the relationship between species cover of *Ranunculus hederaceus* and water chemistry. Both mineral *concentration* and mineral *flux* (concentration × stream velocity) were tested as explanatory variables because it is unlikely that concentrations *per se* are a good measure of mineral availability in running waters. To

check whether outliers had a large influence on the response functions these were recomputed without the two most extreme values (recommended by Jongman *et al.* 1987).

RESULTS

Hydrological relations between Ranunculus hederaceus habitats and the surrounding landscape

In Deurze (Fig. 1) differences in hydraulic head between groundwater and surface water indicated an upward movement of groundwater in the centre of the valley (D3) while the flanks (D1, D2) showed infiltration characteristics. The water level in the ditch remained approximately constant until July when it dried out completely. The ditch was then invaded by large helophytes and algae and *Ranunculus hederaceus* disappeared almost instantaneously.

All groundwater samples were characterized by a high proportion of Ca and SO_4^{2-} , but there were differences in the similarity to lithotrophic groundwater. This figure decreased gradually from D1 to D5 (Fig. 1, Table 1). In fact, the latter samples were chemically more related to rainwater (Table 1). The chemical composition of the surface water showed a great resemblance to the groundwater in D3 (Table 1).

Both the surface water and the groundwater showed high NO_3^- concentrations throughout the spring, while the surface water contained a lot of phosphate as well. *Ranunculus hederaceus* grows in the centre of the seepage area where most nutrient-rich groundwater is welling up.

The ditches in the Gieten area (Fig. 1) contained running water throughout the spring, both in periods of precipitation excess and in periods of precipitation deficit. Differences in hydraulic head between groundwater and surface water indicated upward groundwater movement all along the transect. The water level remained constant throughout the spring, but was much higher in summer when it was manipulated for agricultural purposes.

The surface water belonged to the CaSO_4 type, like most of the groundwater samples. Similarity computations showed that its chemical composition was intermediate between rainwater and lithotrophic water, with the exception of the groundwater in the centre of the valley (G6) which showed a large resemblance to lithotrophic water (Table 1). Samples, taken at three different dates, showed that this gradient was very stable.

The analyses also revealed a stable gradient in the NO_3^- content of the groundwater with high values along the valley flanks to very low figures in the centre (Fig. 1, Table 1). The surface water contained a lot of nitrate as well, comparable to water from the valley flanks (G1, G2). *Ranunculus hederaceus* only grows in the zone where nitrogen-rich water wells up. It is absent in the centre of the valley where nutrient-poor groundwater discharges with a different chemical composition.

In Oudemolen (Fig. 1), differences in hydraulic head between the groundwater and surface water suggested an upward groundwater flow in the middle of the transect (O4 to O2). Along the flanks and close to the brook a neutral situation existed. The surface water level and the stream velocity in the investigated ditch remained constant throughout the growing season.

All groundwater samples belonged to the CaHCO_3 type, however, differing in total mineral contents. The total mineral content increased from the high end of the gradient

(c)

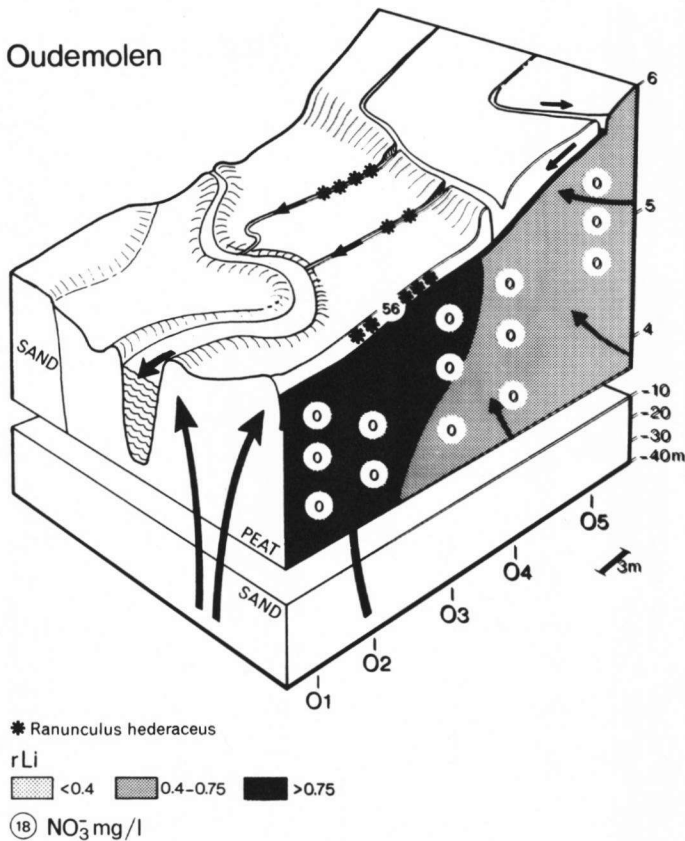


Fig. 1. (c).

Fig. 1. Landscape models of the study areas Deurze, Gieten, Oudemolen, showing the distribution of *Ranunculus hederaceus* in relation to nitrate content of the groundwater, similarity between chemical composition of the groundwater and standard lithotrophic water (rLi) and direction of water flow (black arrows). Presented data are from 24-04-89. Depths shown are in metres above mean sea level.

(O5, O4) towards the lower end (O3, O2, O1) and so did the correlation with lithotrophic water (Table 1). The water quality of the ditch bore hardly any resemblance to the groundwater samples.

In contrast to the groundwater samples, the surface water was rich in nitrogen and phosphate. As *Ranunculus hederaceus* has increased here since its first discovery in 1974 these conditions seem to be favourable for the species.

Species performance in relation to habitat characteristics

Site characteristics. Most surface water sampled from *Ranunculus hederaceus* stands (Table 2) is characterized by a fairly low total mineral content, though not extremely poor. Most parameters showed a large variation with distributions strongly skewed to the right, i.e. with a long tail at the high end of the scale (Table 2). The mean values of P_2O_5 and NO_3^- , SO_4^{2-} and Cl^- are relatively high in comparison to the Dutch water quality standards for fresh (surface) water (CUVWO 1986).

A classification of the water samples on the basis of the nutrient content revealed that most of the samples had a P_2O_5 -concentration below $1 \mu mol l^{-1}$ (Fig. 2), making

Table 1. Hydrochemical characteristics of the study areas Durze, Gieten, Oudemolen as compared to literature data. Similarities to lithotrophic water (rLi), atmotrophic water (rAt) and thalassotrophic water (rTh) are given. For convenience, only data from 24 April 1989 and from 50 cm depth are presented, except where otherwise indicated

Sample	EC ₂₅ µS cm ⁻¹	pH	Ca mm l ⁻¹	Mg mm l ⁻¹	Na mm l ⁻¹	K mm l ⁻¹	HCO ₃ mm l ⁻¹	SO ₄ mm l ⁻¹	Cl mm l ⁻¹	P ₂ O ₅ µm l ⁻¹	NO ₃ µm l ⁻¹	NH ₄ µm l ⁻¹	rLi %	rAt %	rTh %
Lithotrophic standard ¹	652	7.3	2.9	0.3	0.5	0.1	6.6	0.1	0.3				100	-56	30
Atmotrophic standard ¹	50	4.2	0.0	0.0	0.1	0.0	0.0	0.1	0.1				-56	100	-17
Thalassotrophic standard ¹	52000	8.3	10.5	57.6	455.7	10.0	2.0	27.5	538.0				30	-17	100
Durze															
D1	580	6.0	1.6	1.0	1.2	0.2	1.3	0.8	1.2	2.5	2382.4	10.6	61	-17	58
D2	480	5.6	1.5	0.4	0.8	0.5	0.5	0.8	0.9	0.7	1796.6	7.8	51	0	44
D3	480	5.6	1.2	0.7	0.9	0.3	0.5	1.2	0.9	0.9	1357.9	ND	35	19	43
D4	540	5.6	1.6	0.7	0.9	0.3	0.4	1.8	1.0	0.7	436.0	ND	27	30	37
D5	237	5.6	0.4	0.3	1.1	0.4	0.8	0.6	0.9	1.6	1.1	ND	8	45	-13
Surface water	460	6.8	1.4	0.5	0.9	0.4	0.9	0.6	0.5	24.6	1728.2	142.8	64	-13	44
Aquifer (50 m) ^{2,3}	592		1.2								ND				
Gieten															
G1	470	6.0	1.2	0.9	0.9	0.2	1.2	0.7	1.0	1.2	1504.5	0.6	61	14	43
G2	500	6.3	1.5	0.7	0.9	0.1	0.8	1.0	1.2	0.7	1232.1	ND	54	3	43
G3	370	6.8	1.0	0.4	0.9	0.1	1.0	0.9	0.9	0.9	2.3	0.1	49	27	22
G4	390	6.6	1.0	0.2	1.7	0.1	0.8	1.1	1.0	0.9	0.2	0.1	32	44	22
G5	430	6.5	1.1	0.2	1.8	ND	1.3	1.1	1.1	0.9	ND	0.1	46	35	28
G6	253	6.6	1.0	0.2	0.4	ND	1.8	0.2	0.6	1.1	ND	0.1	91	-37	-3
Surface water	440	6.5	1.4	0.6	1.0	0.1	0.8	1.2	0.9	0.7	910.0	ND	44	20	27
Aquifer (60 m) ^{2,3}	167		1.2						0.6		ND				
Oudemolen															
O1	410	5.9	0.4	0.1	0.7	0.1	1.9	0.1	0.5	15.0	ND	0.1	85	-41	54
O2	400	6.3	1.6	0.2	1.0	0.4	3.0	ND	1.0	9.9	ND	ND	94	-51	13
O3	275	6.2	1.0	ND	1.2	0.3	1.9	0.1	1.0	2.9	ND	2.8	80	-30	-2
O4	138	6.1	0.4	0.1	0.7	0.1	1.3	ND	0.5	1.6	ND	ND	72	-31	-19
O5	250	5.5	0.8	0.1	0.6	0.2	0.8	0.3	1.1	1.2	ND	ND	59	1	0
Surface water	555	7.3	0.9	0.5	2.3	0.4	0.6	0.5	3.0	37.5	906.8	350.0	14	20	56
Aquifer (flank) (6 m) ⁴	587	6.3	0.7	0.8	2.0	0.1	0.1	1.6	2.1		664.3	28.6	2	35	
Aquifer (centre) (4 m) ⁴	464	7.5	2.2	0.3	0.3	0.1	4.3	ND	0.5		ND	26.3	99	-42	

ND, not a detectable amount.

Sources: ¹Van Wirdum 1991; ²WRGOD 1978; ³Anonymous 1985; ⁴Grootjans *et al.* 1987.

Table 2. Hydrochemical characteristics of the investigated surface waters, inhabited by *Ranunculus hederaceus*

	Units	n	Mean	SD	CV	Min	Max	Skewness	CUWVO
EC ₂₅	μS cm ⁻¹	31	385.2	128.1	33.3	143.0	707.0		.
pH		31	6.8	0.6	9.4	5.3	8.3		.
Temperature	°C	31	9.2	1.7	18.1	6.7	15.5	R (***)	.
HCO ₃	μM l ⁻¹	31	1440.4	1168.1	81.1	10.0	4759.2	R (**)	.
Na	μM l ⁻¹	31	827.0	434.0	52.5	207.9	1848.2		.
K	μM l ⁻¹	31	294.2	472.8	160.7	0.7	2103.6	R (***)	.
Mg	μM l ⁻¹	31	295.4	158.3	53.6	102.3	721.7	R (*)	.
Ca	μM l ⁻¹	31	843.6	425.9	50.5	163.6	1849.2		0
P ₂ O ₅	μM l ⁻¹	31	3.6	9.6	266.0	0.4	51.1	R (***)	+
NO ₃	μM l ⁻¹	31	285.9	425.3	148.7	0.0	1614.6	R (***)	+
NH ₄	μM l ⁻¹	31	23.2	28.6	123.1	0.1	101.6	R (***)	.
SO ₄	μM l ⁻¹	31	403.7	341.5	84.6	4.0	1199.7		+
Cl	μM l ⁻¹	31	976.1	617.9	63.3	192.4	2613.5	R (*)	+

n, sample number.

SD, standard deviation.

CV, coefficient of variation.

R (***)/L(***), skewness coefficient differs significantly from zero, to the right (R) or to the left (L).

*, P<0.05; ** P<0.01; *** P<0.001.

CUWVO, comparison of mean values to standards for fresh surface water in The Netherlands (CUWVO 1986).

., No standard given.

-, Mean value more than 25% lower than standard.

+, Mean value more than 25% higher than standard.

0, Mean value within 25% interval around the standard.

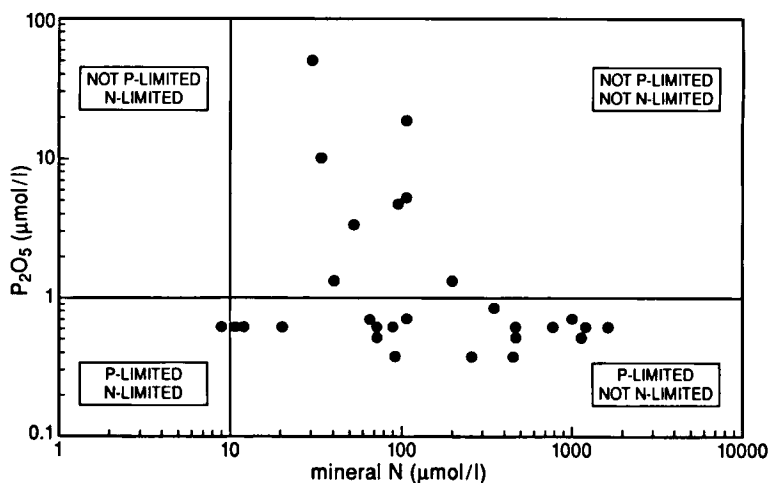


Fig. 2. Relationship between nitrogen and phosphorus content of the surface water at the investigated sites. Limits for nutrient limitation (Bloemendaal & Roelofs 1988) are included.

P-limitation probable (Bloemendaal & Roelofs 1988). Only the samples from the dune edge near Schoorl contained more phosphate. No limiting factor could be found here.

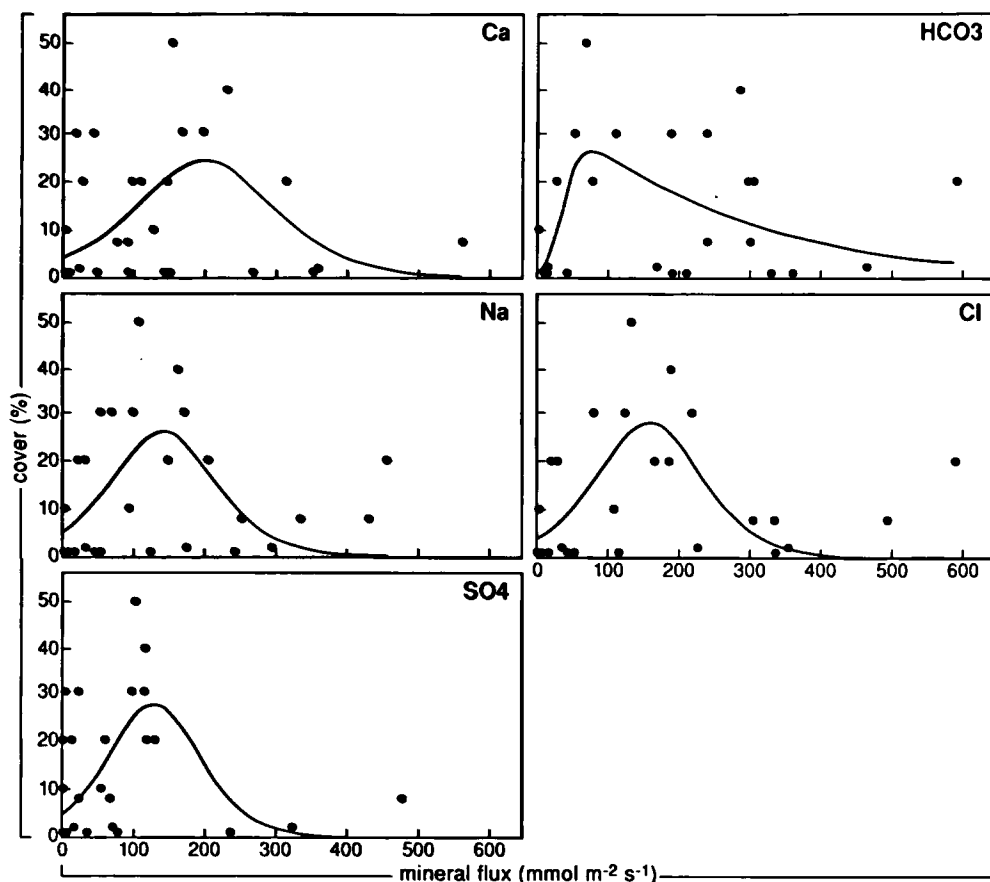


Fig. 3. Cover (%) of *Ranunculus hederaceus* in relation to mineral flux of the surface water. Based on 27 observations (closed dots) from seven study areas. Only significant relations are shown: calcium ($R^2=0.19$); bicarbonate ($R^2=0.22$); sodium ($R^2=0.23$); chloride ($R^2=0.33$); sulphate ($R^2=0.32$).

Response analysis. No significant relations between the cover of *Ranunculus hederaceus* and the chemical composition of the surface water as such were found in the present data set. However, when mineral flux was considered, differences in the cover of *Ranunculus hederaceus* were correlated to differences in the fluxes of Ca^{2+} , HCO_3^- , Na^+ , Cl^- and SO_4^{2-} (Fig. 3). Apart from HCO_3^- , skewed models did not explain significantly more variance than symmetric curves. Omission of the two most extreme values gave practically the same results, so it was concluded that these higher values hardly affected the regressions. The coefficient of determination (19, 22, 23, 33 and 32%) showed that a great deal of the observed variation remained unexplained.

DISCUSSION

Distribution of Ranunculus hederaceus in relation to hydrological systems

Most of the water samples from the present study sites can be classified as 'soft water' or 'fairly soft water' (classification cf. Stuyfzand 1989). Therefore, *Ranunculus hederaceus* may indeed be considered as an indicator of rather mineral-poor water. At

the same time both the water depth and the chemical composition were constant during the vegetation season, as already pointed out by Segal (1966). Constant water levels are considered to be characteristic of water courses which are predominantly fed by upwelling groundwater (Strahler & Strahler 1987). The most stable conditions are found in the discharge areas of large groundwater systems (Engelen & Jones 1986) but in The Netherlands these are always characterized by mineral-rich ('hard') water. Mineral-poor water is found in shallow hydrological systems when the groundwater has only passed through decalcified upper layers. Such systems generally have a small infiltration area and decrease significantly in the dry season (Engelen & Jones 1986). Therefore, the combination 'mineral poor' and 'constant supply' seems contradictory under the Dutch circumstances.

Two hydrogeological configurations can be imagined that prevent the groundwater in larger infiltration areas from penetrating deeper strata. Deurze is an example where a very thick clay layer close to the surface (WRGOD 1978) forces the groundwater to flow laterally. Due to the (fixed) position of this impermeable layer, the groundwater always discharges in the same zone ('stationary' buffering). The upwelling groundwater has infiltrated nearby and the nutrients it contains must be the result of the application of fertilizer to the surrounding fields.

Gieten and Oudemolen are examples of a situation where a very large hydrological system underlies a smaller one. As the size of the large system is practically independent of the precipitation surplus during the previous season (Engelen & Jones 1986), the groundwater of the smaller system is always forced to the surface in the same border zone ('dynamic' buffering). Extensive hydrological research (Grootjans *et al.* 1987) has shown that in Oudemolen there are indeed two different groundwater flows reaching the surface. The first one is a lateral flow that originates in the surrounding arable fields and wells up along the valley flanks. This water is of the NaSO_4 type and is rich in nutrients (Table 1). In the centre of the valley, water from deeper layers wells up. It is of the CaHCO_3 type and shows a high resemblance to the lithotrophic standard. The present study shows this gradient in more detail: the resemblance of the phreatic water to deeper groundwater increases from flank to valley centre. The surface water in the ditch shows little resemblance to this upwelling water, however, but looks very much like the lateral flow instead. This leads to the conclusion that nutrient-rich water from the flanks enters the valley through the drainage system. *Ranunculus hederaceus* occurs along this gradient, just within the reach of the nutrient-rich water. In Gieten somewhat less data are available, but it is here evident as well that *Ranunculus hederaceus* occurs in a border zone between two hydrological systems (WRGOD 1978).

Nutritional conditions

In freshwater ecosystems four resources (inorganic C, N, P and light intensity) are considered as potentially limiting factors for plant growth (Wiegand 1980; Roelofs 1983; Bloemendaal & Roelofs 1988). Bloemendaal & Roelofs (1988) consider $100 \mu\text{mol l}^{-1}$ for C, $10 \mu\text{mol l}^{-1}$ for N and $1 \mu\text{mol l}^{-1}$ for P as boundary values beneath which the resource is limiting. Pott (1983) gives comparable values for N and P for boundaries between mesotrophic and eutrophic stands ($70 \mu\text{mol l}^{-1}$ for N and $3.5 \mu\text{mol l}^{-1}$ for P, respectively).

Both C- and N-limitation are unlikely in the case of *Ranunculus hederaceus* as the C- and N-contents of the water lie well above the given thresholds in all samples. Moreover, Wiegand & Herr (1984) consider floating leaves in *Ranunculus* species as an

adaptation to growing in HCO_3^- -poor water, because the species can take CO_2 from the air.

The foregoing could imply that P is mostly limiting biomass production. Indeed, many *Ranunculus hederaceus* stands are found in surface water in P-concentrations below $1 \mu\text{mol l}^{-1}$. One should then expect a positive correlation between the phosphorus content of the water and biomass production. However, neither P-concentration, nor P-flux showed any significant relation to the cover of *Ranunculus hederaceus*. Obviously, a higher P-flux of the water does not lead to a higher biomass production. A similar result was achieved in experimental studies (Caines 1965; Howard-Williams 1981; Spink *et al.* 1993) where addition of P to the water phase did not result in a higher biomass production. Therefore, many authors (Bristow & Whitcombe 1971; Denny 1972; Best & Mantai 1978; Carignan & Kalff 1980; Huebert & Gorham 1983) consider the soil as the main P-source for aquatic macrophytes, especially when the water is phosphate poor. In the present study, however, this is very unlikely as the soil consisted of oligotrophic cover sands (De Bakker 1979). Moreover, in the case of upwelling groundwater the surface water has the same chemical composition as the interstitial water around the plants' roots.

Although *Ranunculus hederaceus* generally inhabits small brooklets, running water per se does not seem to be an absolute prerequisite, since it is also found on wet and sandy soils. By its occurrence in running waters the species seems to avoid competition. *Ranunculus hederaceus* is a poor competitor with a strongly reduced vitality under shaded conditions (Cook 1966; De Sloover *et al.* 1977). The experimental reduction of stream velocity by Spink (1992) caused a substantial decline of the related *Ranunculus penicillatus* in favour of the strong competitor *Elodea canadensis* due to competition for light. Other experiments by Spink *et al.* (1993) showed that *Ranunculus hederaceus* became outcompeted after eutrophication even under 'normal' stream velocities. A fivefold increase of available phosphate caused a tremendous increase of filamentous algae and a corresponding decrease of *Ranunculus hederaceus*. Also, field observations in the present study showed that the water courses in the study areas became indeed invaded by algae and large helophytes, such as *Glyceria notata* and *Phragmites australis*, as soon as the water became stagnant in the summer. *Ranunculus hederaceus* then disappeared quickly. If this happens before the seeds have been formed, the resettlement of this annual species comes into danger (De Sloover *et al.* 1977).

Ranunculus hederaceus as an indicator of landscape changes

From the foregoing, the optimal environment of *Ranunculus hederaceus* appears to be stable, mineral-poor and, if total fluxes instead of mere concentrations are considered, nutrient-rich. Such conditions are not difficult to find separately, but it is the combination that makes the potential habitats so scarce. Nutrient-rich conditions are typical for dynamic environments, while stable environments are generally associated with poorer conditions (Van Leeuwen 1966).

At present, all *Ranunculus hederaceus* habitats in The Netherlands are man-made ditches which are cleaned every autumn, thereby creating a suitable environment for pioneer species. The nutrient-rich conditions in which it grows are the result of excessive fertilization in the infiltration areas (Bleuten 1990; Billwitz 1991). Near Gieten even the hydrological gradient itself has a human origin. Before the beginning of this century the whole valley was filled with a large bog on top of a former seepage area (Casparie 1972).

It was the peat cutting that reactivated the seepage belt and created the gradient described in this paper.

Rare plants generally become rarer as human influence increases (Westhoff 1979), but in the case of *Ranunculus hederaceus* it may well be doubted whether this species was more common under natural conditions. Almost certainly the desired stable water levels did exist in many places, but probably the nutrient content was too low. Natural habitats are imaginable at spots where nutrients were added to the system by wild animals. Cook (1966) described sites in the chalk district in England where *Ranunculus hederaceus* was found at drinking places of cattle, where the nutrient-poor conditions were relieved by the addition of excrements and urine. When humans started exploiting the landscape by agricultural practices many water courses became more nutrient-rich. *Ranunculus hederaceus* could probably colonize new habitats following human activities. An example was witnessed in the area around Gieten (P.C. Schipper, personal communication). Although *Ranunculus hederaceus* has been present in the area for a few decades it was rare. The number of stands could increase considerably when the farmers in this region started to grow corn about 10 years ago. At present it seems to become rarer, possibly because of too high a nutrient level (Segal 1966; De Sloover *et al.* 1977).

To summarize the discussion on the indicative value of *Ranunculus hederaceus* the situation near Oudemolen can serve as an example. Geohydrological research (WR-GOD 1978) indicated that this area was nourished by upwelling Ca-rich, nutrient-poor groundwater. *Ranunculus hederaceus* was not expected at this site but, in fact, the species was found there in 1974 and has increased ever since. Detailed investigations (Bakker & Grootjans 1991) showed that drainage had diverted the deep groundwater flow towards the brook, giving way to a nutrient-rich lateral flow from the adjoining agricultural fields. Hence, the increase of a rare plant species like *Ranunculus hederaceus* does not always indicate the well-being of a nature reserve.

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