

KWR 2014.054 | June 2014

Manual and description of ESTAR, version 01

A software tool to analyse vegetation plots



Manual and description of ESTAR, version 01

A software tool to analyse vegetation plots

KWR 2014.054 | June 2014

Project number

400581/004/004

Project manager

G. van den Berg

Quality Assurance

E. Dorland

Authors

J.P.M. Witte, R.P. Bartholomeus, D.G. Cirkel, E.
Doomernik, Y. Fujita, J. Runhaar

Year of publishing
2014

More information

T +31(0)306069647
E flip.witte@kwrwater.nl

PO Box 1072
3430 BB Nieuwegein
The Netherlands

T +31 (0)30 60 69 511
F +31 (0)30 60 61 165
E info@kwrwater.nl
I www.kwrwater.nl



Watercycle
Research
Institute

KWR | June 2014 © KWR

Alle rechten voorbehouden.
Niets uit deze uitgave mag worden verveelvoudigd,
opgeslagen in een geautomatiseerd gegevensbestand,
of openbaar gemaakt, in enige vorm of op enige wijze,
hetzij elektronisch, mechanisch, door fotokopieën,
opnamen, of enig andere manier, zonder voorafgaande
schriftelijke toestemming van de uitgever.

Contents

1	Introduction: what is ESTAR?	5
2	Manual	7
2.1	Files you need to run ESTAR	7
2.2	Description of the input file with relevés	7
2.3	Settings of ESTAR	7
2.4	Running the program	8
2.5	Reading the output file	8
3	Content information	9
3.1	Introduction	9
3.2	The list of indicator values of species (ESTAR.CSV)	9
3.3	Average indicator values of relevés	11
3.4	From average indicator values to physical variables	12
4	Concluding remarks	17
	References	19
	Appendix: Ecological species groups and indicator values	23

1 Introduction: what is ESTAR?

ESTAR (Eco-Statistical Tool to Analyse Relevés) is a software tool to analyse vegetation plots (relevés). Input to ESTAR is a simple list of relevés. Output is a list with ecological information about each relevé, such as the division of each relevé into ecological classes for moisture regime ('aquatic', 'wet', 'moist' and 'dry'), and the average indicator values for Salinity, Moisture regime, Nutrient-availability and Acidity (mS , mF , mN , mR , respectively). Moreover, on the basis of these indicator values ESTAR produces estimates of soil pH, average groundwater depth, and other physical variables.

Next chapter (2) is a short manual of ESTAR. The content of ESTAR is described in Chapter 3. Chapter 4 shows some applications, as well as our plans to further improve this tool.



2 Manual

2.1 Files you need to run ESTAR

After installing ESTAR the following files are available at the working directory:

1. ESTAR.EXE
2. ESTAR.INI
3. ESTAR.CSV
4. CURVES.TXT

Of course, you also need an input file containing information about the relevés you want to process. An example is provided after installing ESTAR:

5. InputExample.csv

Next section describes the features of input files.

2.2 Description of the input file with relevés

As input, ESTAR requires a Comma-Separated Value file (*.csv) with relevés.

The first record of this file is designated for information about the project. You may, for instance, write the name of the project on this record, and of the researcher that collected the relevés. Example:

This is an input test file for ESTAR made by the development team of KWR, 12 June 2014

Each of the following records should contain the following information:

Relevé code, Species number AND/OR Species name, Species cover (%).

These variables should be separated by a comma or semicolon. The decimal sign can be either a dot, or a comma. The program performs its computation on the basis of either species names, or species numbers. Hence, for a record containing relevé number 21 and species number 66 (*Anthoxanthum odoratum*) with a cover of two-and-a-half percent, some valid input formats are:

- 21,66, *Anthoxanthum odoratum*,2.5
- 21,66,2,5
- 21,*Anthoxanthum odoratum*,2.5

Most likely you want to run the program on the basis of species numbers, since species names can easily be misspelled. The file ESTAR.csv, provided with the program, contains a complete list of all species numbers and species names that ESTAR utilizes.

Species cover (and abundance) is usually recorded in a scale consisting of classes, for instance the scale of Braun-Blanquet (Mueller-Dombois & Ellenberg, 1974; Van der Maarel & Franklin, 2012). You have to convert these classes to percentages yourself; if you do not intend to give a weight to species cover, you may put a dummy value (e.g. 99.) in the last column of the input file.

2.3 Settings of ESTAR

After starting the program, you first have to define the setting of the input and output files. Most of the options are self-evident, except for the following:

- **Search by.** In a pull-down menu, you can choose between two options: 'species name' and 'species number'. With this choice you decide whether ESTAR uses either species names or species number in the input file as entries for its look-up-table with species information. Most likely you want to run the program on the basis of species numbers, since species names can

easily be misspelled. The file ESTAR.csv, provided with the program, contains a complete list of all species numbers and species names that ESTAR utilizes.

- **Minimum number of species.** You may want to define a minimum number of species (e.g. 2 or 3) with known indicator values in order to obtain reliable estimates about mean indicator values of relevés.
- **Weight species cover.** With a pull-down menu, ESTAR offers three ways to weigh species cover in the computation of plot mean indicator values (section 3.3):
 1. no weighing of cover
 2. weighing proportionate to species cover
 3. weighing according to the method of Käfer and Witte (2004)

Choose option (1) if you want ESTAR to calculate physical variables, like soil pH, because relationships between indicator values and environmental variables were derived on the basis of this method.

Warning: if you do not define the setting according to the setup of your computer and the relevé input file, ESTAR will produce unusable results. This can e.g. be recognized by empty columns in the output file.

2.4 Running the program

Go to the Run menu and:

1. Select path and name of the input file
2. Select path and write name of the output file
3. Push the **Run** button

2.5 Reading the output file

The output file has a csv format. Line 1-11 contain general information about ESTAR and its settings. When you open this file in Excel and successively place the data in separate columns (In Excel: on the Data tab, in the Data Tools group, click Text to Columns), the columns have the following meaning:

- A Relevé number
- B Number of species in relevé
- C Number of species with known indicator value in relevé
- E-S Percentage of species from different ecological groups (description: § 3.2)
 - E-G Species of 'fresh', 'brackish' and 'alkaline' sites
 - H-K Species of '(semi-)aquatic', 'wet', 'moist' and 'dry' sites
 - L-O Species of 'nutrient-poor', 'moderately nutrient-rich and alkaline', 'moderately nutrient-rich and not alkaline', and 'very nutrient-rich' sites
 - P-S Species of 'acid', 'weakly acid', 'alkaline' sites, and 'species not indicative for acidity'
- U-X Plot mean indicator value for 'salinity' mS, 'moisture regime' mF, 'nutrient availability' mN, and 'acidity' mR. The scale of the indicator values ranges from 1 to 3 (*S*, *N*, *R*) or 4 (*F*). See § 3.2 and Figure 1.
- Z-AZ Physical variables derived from mean indicator values (U-X) or ecological groups (E-S). For each variable, the best estimate is given, together with a band-width in terms of *RMSE* (Root Mean Square of Errors; § 3.4.1). A dummy value of 999 denotes that a physical variable could not be computed by ESTAR.
 - Z-AB Salinity (§ 3.4.2). Not defined yet in ESTAR, so all records contain the dummy value of 999.
 - AD-AF Moisture regime in terms of average groundwater level in springtime *MSL* (§ 3.4.3.1)
 - AH-AJ Moisture regime in terms of oxygen stress (§ 3.4.3.2)
 - AL-AN Moisture regime in terms of drought (§ 3.4.3.3)
 - AP-AR Nutrient availability in terms of P-mineralization on a mass basis (§ 3.4.4)
 - AT-AV Nutrient availability in terms of P-mineralization on a volume basis (§ 3.4.4)
 - AX-AZ Soil-pH (§ 3.4.5)

3 Content information

3.1 Introduction

Core of ESTAR is a list of indicator values, which is described in the following section (§ 3.2). These indicator values have been derived from the ecological species groups for the Netherlands and Flanders by Runhaar *et al.* (2004), in which species have been grouped per ecosystem type. A description of the ecosystem types and the species characteristic for these ecosystem types can be found in the Appendix. In the next section (§ 3.3), we will explain how ESTAR computes fractions of ecological classes, such as 'wet', 'moist', 'acid', as well as average indicator values of relevés. After that (§ 3.4) we will explain how ESTAR uses these fractions and average indicator values to obtain estimates of physical soil and water variables, such as soil-pH and groundwater depth.

3.2 The list of indicator values of species (ESTAR.CSV)

On the basis of the ecological species groups, Witte *et al.* (2007) computed indicator values of plant species (vascular plants, mosses and lichens). In the Appendix of this manuscript we describe the ecological species groups and the underlying ecosystem classification, as well as how indicator values for plant species were obtained from this system.

The list of indicator values of plant species is given in the file ESTAR.CSV. Table 1 shows the first six species of this file. Four site factors of the ecotope system can be distinguished, namely: (1) Salinity, (2) Moisture regime, (3) Nutrient availability and (4) Acidity. Within each site factor, a number of ecological classes are distinguished:

1. Salinity
 - a. fresh
 - b. brackish
 - c. saline
2. Moisture regime
 - a. water
 - b. wet
 - c. moist
 - d. dry
3. Nutrient availability
 - a. nutrient-poor
 - b. moderately nutrient-rich alkaline
 - c. moderately nutrient-rich not alkaline
 - d. very nutrient-rich
4. Acidity
 - a. acid
 - b. weakly-acid
 - c. alkaline
 - d. indifferent

Table 1. Part of the list of indicator values, showing the first six plant species.

Species		1. Salinity										2. Moisture regime										3. Nutrient availability										4. Acidity									
		fresh			brackish			saline			indicator value S	weight W _S			(semi)aquatic	wet	moist	dry	indicator value F	weight W _F			nutrient-poor	moderately rich alkaline			moderately rich not alkaline			very nutrient rich	indicator value N	weight W _N			acid	weakly acid	alkaline	unknown	indicator value R	weight W _R	
number name	1	Acer	campestre	1.00	0.00	0.00	1.00	1.00	0.00	0.00	0.80	0.21	3.21	1.00	0.50	0.00	0.30	0.21	1.71	1.00	0.00	0.00	0.00	0.29	0.13	1.56	1.00	0.00	0.00	0.00	0.26	0.32	0.43	2.55	0.62						
	2	Acer	pseudoplatanus	1.00	0.00	0.00	1.00	1.00	0.00	0.00	0.66	0.34	3.34	1.00	0.58	0.00	0.00	0.29	0.13	1.56	1.00	0.00	0.00	0.00	0.26	0.32	0.43	2.55	0.62												
	3	Aceras	anthrophophorum	1.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00	3.00	1.00	1.00	0.00	0.00	0.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00	3.00	1.00									
	4	Achillea	millefolium	1.00	0.00	0.00	1.00	1.00	0.00	0.00	0.36	0.64	3.64	1.00	0.00	0.00	1.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	2.50	0.10													
	5	Achillea	ptarmica	1.00	0.00	0.00	1.00	1.00	0.00	0.68	0.32	0.00	2.33	1.00	0.00	0.00	1.00	0.00	2.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	2.50	0.10													
	6	Aconitum	vulparia	1.00	0.00	0.00	1.00	1.00	0.00	0.00	1.00	0.00	3.00	1.00	1.00	0.00	0.00	0.00	1.00	1.00	0.00	0.00	0.00	0.00	0.00	1.00	0.00	3.00	1.00												

The preference of each species for each of these classes is expressed as a fraction f . For instance *Acer pseudoplatanus* (species number 2 in Table 1) is ascribed for:

$f_{\text{salinity}} = 1.0$ to 'fresh',

$f_{\text{moisture}} = 0.66$ and 0.34 to 'moist' and 'dry'

$f_{\text{nutrients}} = 0.58$, 0.29 and 0.13 to 'nutrient-poor', 'moderately rich not alkaline' and 'very nutrient rich'

$f_{\text{acidity}} = 0.26$, 0.32 and 0.43 to 'weakly acid', 'alkaline' and 'indifferent'

The fractions of all classes from a particular site factor are added together always 1.0. For each characteristic, Table 1 also provides indicator values iv for Salinity (S), Moisture regime (F), nutrient availability (N) and for Acidity (R): $IV = [S, F, N, R]$. The scale of the indicator values ranges from 1 to 3 (S , N , R) or 4 (F). Compared to the 1-9 scale (1-12 for moisture) of Ellenberg (1992), these scales are rather short. This has, however, no substantive meaning. In contrast to Ellenberg's scale, Table 1 presents values in two decimals. Figure 1 shows the interpretation of the indicator value scales of ESTAR.

Each species can be assigned to more than one ecological species group. The larger the number of species groups is, the less the indicative value of a species. To account for this, also weights W^v were ascribed to the indicator values of each species. For example, *Acer pseudoplatanus* has a weight $W^N = 1.00$ for Nutrient-availability, and a weight $W^R = 0.62$ for Acidity, meaning that it is more indicative for the nutrient status than for the acidity of the soil.

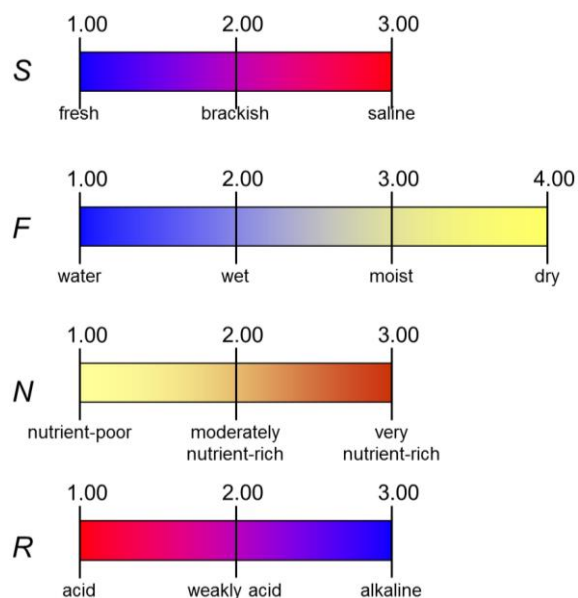


Figure 1. Visual presentation of the indicator value scale for the site factors Salinity S , Moisture regime F , Nutrient availability N , and Acidity R , applied in ESTAR.

For more information on the ecological species groups and the methods to derive f , iv , and W^v , we refer to the Appendix.

3.3 Average indicator values of relevés

For each relevé, containing n species s , ESTAR computes as follows the percentage P of ecological class k to characterize the relevé:

$$P(k) = 100 \frac{\sum_{s=1,n} W^c(c) \times f(k)}{\sum_{s=1,n} W^c(c)} \quad [1]$$

Where W^c is a weighing function for vegetation cover c . The percentages P of all classes from a particular site factor are added together always 100. ESTAR offers three options for weighing species cover c (%) (Figure 2):

1. no weight is given to species cover (the 'qualitative method' *sensu* Ellenberg (1992)): $W^c = 1$.
2. species are weighted proportionate to their cover (the 'quantitative method' *sensu* Ellenberg (1992)): $W^c = c$
3. species are weighted according to the method of Käfer and Witte (2004): $W^c = \min(1, 0.5 + 0.0057c)$

In practice, the results of the qualitative method 2 much resembles option 3. The quantitative method is not recommended for general use (Ellenberg, 1992; Käfer & Witte, 2004), but can be useful in specific situations. For example, to monitor the short-term effects of interventions in situations where the time-period is too short to expect changes in species composition, but long enough to expect changes in abundance of species belonging to a certain ecological group.

Indicator values of relevés are computed as weighted means, using the weights for indicator values W^v and cover W^c as follows:

$$mIV = \frac{\sum_{s=1,n} W^c \times W^{IV} \times IV}{\sum_{s=1,n} W^c \times W^{IV}} \quad [2]$$

In this way, mean values for Salinity, Moisture regime, Nutrient-availability and Acidity are obtained: mS , mF , mN , and mR .

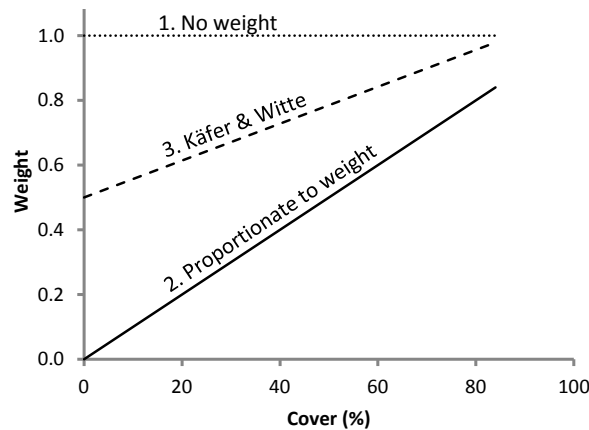


Figure 2. Three methods to weigh species cover in ESTAR.

The user may enter relevés containing species for which no ecological information is available in ESTAR, or relevés that are extremely poor in species. To prevent unreliable calculations, the user has to specify how much species with known indicator values should at least be present in the relevé. When this minimum number is not reached, ESTAR produces dummy values '999' for the relevé.

3.4 From average indicator values to physical variables

3.4.1 Introduction

Plot mean indicator values have been regressed against physical and chemical variables observed or simulated in vegetation plots, such as mean Spring groundwater level (*MSL*) and soil pH. ESTAR uses these empirical relationships inversely to estimate *MSL* from *mF*, soil pH from *mR*, etc. These estimates are presented including their Root Mean Square of Error *RMSE*:

$$RMSE = \frac{1}{n} \sqrt{\sum (y_{obs} - y_{exp})^2} \quad [3]$$

Where *n* is the number of observations, y_{obs} is the observed physical variable and y_{exp} is the physical variable predicted with the empirical relationship. Regression was performed by minimizing the sum of squares, using the Levenberg-Marquardt algorithm (Marquardt, 1963).

3.4.2 Salinity

Currently ESTAR is not able to express salinity in a quantitative variable, since field data are lacking to correlate *mS* to a proxy of salinity, such as chlorine content of soil moisture in the root zone of plants.

3.4.3 Moisture regime

3.4.3.1 Mean groundwater level in Spring, *MSL*

Soil moisture affects plant performance both when it is deficient (drought stress) and when it is superfluous (oxygen stress). The mechanisms through which these stresses act are highly different. Drought stress limits the photosynthetic activity of plants, whereas oxygen stress limits the metabolic activity of plants by decreased root respiration (Bartholomeus *et al.*, 2011b). If we focus on plant communities from groundwater dependent sites, where the soil oxygen status is a primary determinant of plant performance, the groundwater depth relative to soil surface may be considered as a good proxy of *mF*. On the basis of 145 vegetation plots from Runhaar (1989) and Staatsbosbeheer (Beets *et al.*, 2003), Bartholomeus *et al.* (2012) derived a relationship between mean groundwater level in Spring, *MSL*, and *mF* for terrestrial vegetation (i.e. with $mF > 1.75$). Here we use the data of Bartholomeus *et al.* (2012) to describe *MSL* as a function of *mF*. Since vegetation is independent of the groundwater at deeper groundwater depths, we only use plots from plant communities of wet to moist conditions, i.e. with $mF < 3.20$ (Figure 3):

$$MSL = 72.268 - 38.08mF | 1.75 < mF < 3.20 \quad (N = 120, R^2 = 54\%, RMSE = 12.5 \text{ cm}) \quad [4]$$

3.4.3.2 Respiration stress, *RS*

Therefore, we introduced a climate-robust measure of oxygen stress: respiration stress (Bartholomeus *et al.*, 2012). The respiration stress, *RS* ($\text{kg O}_2 \text{ m}^{-2} \text{ 10d}^{-1}$), is based on the most direct vegetation response to soil oxygen deficiency, and involves the relevant processes in the soil-plant-atmosphere continuum. Root respiration is determined by interacting respiratory (i.e. oxygen consuming) and diffusive (i.e. oxygen providing) processes in and to the soil. Plant roots respire at a potential rate under optimal soil aeration and thus non-limiting oxygen availability. Upon increasingly wetter conditions, however, the gas-filled porosity of the soil decreases and oxygen availability becomes insufficient for potential root respiration.

Daily respiration reduction (i.e. potential minus actual respiration) can be simulated with the 'oxygen model' of Bartholomeus *et al.* (2008b), which uses generally applied physiological and physical relationships to calculate both the oxygen demand of, and the oxygen supply to plant roots. As a

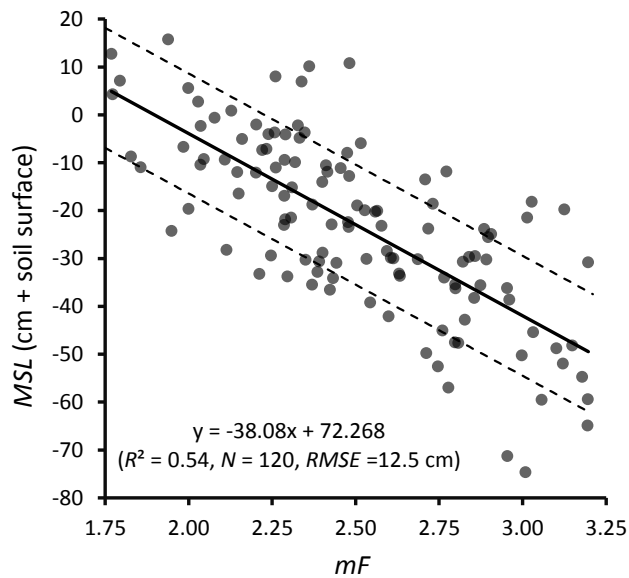


Figure 3. Relationship between average moisture indication mF and mean groundwater level in spring MSL (+/- RMSE). Data from Bartholomeus *et al.* (2012).

measure of oxygen stress, we used the yearly maximum reduction in respiration across a 10-day period, averaged over 30 years. This measure (RS) enables us to account for the effects of both extreme rainfall events and high temperatures, as especially the combination of these conditions affects vegetation.

Bartholomeus *et al.* (2012) derived a relationship between RS and mF based on the same 145 vegetation plots as used for MSL vs. mF . Here we use the data of Bartholomeus *et al.* (2012) to describe RS as a function of mF . To prevent the prediction of negative RS -values, this function is only applicable at $mF < 3.75$ (Figure 4):

$$RS = 0.0796 - 0.0212mF \mid 1.75 < mF < 3.75 (N = 145, R^2 = 75\%, RMSE = 0.006 \text{ kg O}_2\text{m}^{-2}\text{10d}^{-1}) \quad [5]$$

It is remarkable that RS and mF are well correlated along the whole gradient of the 145 vegetation plots. This is because RS is correlated to drought stress: the finer the soil texture, the higher the oxygen stress, but the lower drought stress as well, and *vice versa*.

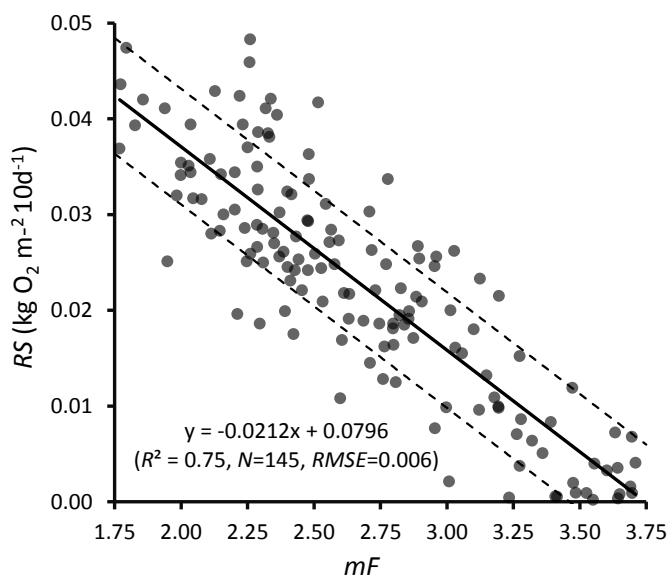


Figure 4. Relationship between average moisture indication mF and respiration stress RS (+/- RMSE). Data from Bartholomeus *et al.* (2012).

3.4.3.3 Drought stress, TS

Drought stress as a result of low soil moisture contents inhibits plant transpiration, a process that also responds to increased temperatures and atmospheric CO_2 -concentrations. As a result of increased stomatal closure, to reduce water loss by transpiration, both photosynthesis and cooling are negatively affected. Species may be able to grow on very dry sites due to a succulent structure or by reducing the transpirational water loss by having hairy leaves.

Fraction of dry species f_{dry} (xerophytes) is used as explanatory variable for drought stress, the latter being defined as the maximum transpiration deficit of a standard grassland during 10 successive days, averaged over 30 years (equivalent to the calculation of RS). On the basis of data of Runhaar (1989), De Jong (1997), Jansen *et al.* (2000), Beets *et al.* (2003) and Jansen and Runhaar (2005), Bartholomeus *et al.* (2011b) derived a relationship between TS and f_{dry} . Here we use the data of Bartholomeus *et al.* (2011b) to describe TS as a function of f_{dry} . This function is not applicable to plant communities with a very low fraction of xerophytes, i.e. with $f_{dry} < 0.1$ (Figure 5):

$$TS = 0.034f_{dry} - 0.00181 \mid f_{dry} > 0.1 (N=114, R^2 = 45\%, RMSE = 0.0075 \text{ m } 10d^{-1}) \quad [6]$$

3.4.4 Nutrient availability

The availability of nutrients is one of the soil factors which influence plant performance. Among several macronutrients, nitrogen (N) and phosphorus (P) are recognized as the most essential nutrients for plant growth. Although availability of N and P are typically correlated, P availability was more strongly related to N_m than N availability (Fujita *et al.*, 2013a). Nutrient availability of a site changes over time and therefore is evaluated differently depending on the time scale of question (such as dissolved amount of the nutrient at a certain moment, nutrient mineralization rates during a certain period, or total pool size of the nutrient at an equilibrium status). Fujita *et al.* (2013a) showed that the time scale had a minor influence on the relationships between nutrient availability and mN , yet longer term expressions (such as multiple-year mineralization rates) tended to show slightly better relationships.

For these reasons, we used mineralization rates of P as a proxy for the nutrient availability of 36 plots that were recorded in 2011. Fujita *et al.* (2013a) simulated these rates on a mass basis (mg P kg soil^{-1}) for the top 10 cm of the soil with the soil organic matter model Century (Parton *et al.*, 1993) which was adapted by Fujita *et al.* (2013b) to groundwater dependent sites. Geochemical processes of inorganic P (e.g. adsorption) were not included in this model, possibly causing unrealistic estimates of P

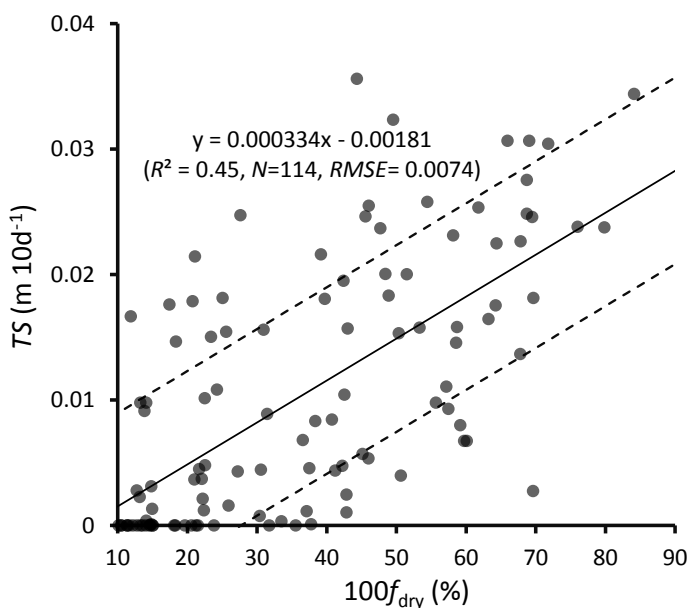


Figure 5. Relationship between percentage of xerophytes f_{dry} and drought stress TS (+/- RMSE). Data from Bartholomeus *et al.* (2012).

mineralization rates for some plots. Using the dataset of Fujita *et al.* (2013a), we derived the following relationship between mN and P mineralization (Figure 6, left):

$$\ln(P_{\min}^m + e) = 1.05mN + 0.07 | mN < 2.5 (N = 36, R^2 = 56\%, RMSE = 0.34) \quad [7]$$

Where P_{\min}^m is the average simulated P mineralization rate on a mass basis (mg P kg soil⁻¹y⁻¹) over 5 years prior to vegetation recording (2006-2011). Since some of the sites had net P immobilization (negative values) instead of net P mineralization, the mathematical constant of the natural logarithm e (~ 2.718) was added to make $P_{\min}^m + e$ to always be a positive value. We restricted the prediction of P_{\min}^m to an mN range till 2.5, as the highest mN value in the dataset of Fujita *et al.* (2013a) was 2.44.

We may argue that for plant roots the amount of P released per unit of soil volume is more relevant than the P-mineralization on a mass basis. Therefore we multiplied the latter with the bulk density of the soil (thus introducing an additional source of uncertainty), in order to express the mineralization rate per dm³ soil (Figure 6, right):

$$\ln(P_{\min}^v + e) = 0.95mN + 0.18 | mN < 2.5 (N = 36, R^2 = 55\%, RMSE = 0.31) \quad [8]$$

Where P_{\min}^v is the P mineralization rate on a volume basis (mg P dm soil⁻³ y⁻¹) (Figure 6, right).

3.4.5 Acidity

Soil acidity is a well-known factor controlling the species composition of natural plant communities (Ellenberg, 1992). Although a low pH (high proton concentrations) is toxic to plants, indirect effects of soil acidity prevail. Important soil acidity controlled site factors are for instance aluminium, manganese and iron toxicity and phosphorous, iron, calcium and potassium deficiencies (Poozesh *et al.*, 2007). Adaptations of plants to high and low soil pH involve complex biochemical, physiological and mutualistic pathways, allowing adapted species to survive harsh chemical environments. Adaptations to acid mineral soils include root-induced changes in the rhizosphere, such as release of chelators for Al, higher activity of ectoenzymes, and increase in root surface area via mycorrhiza (Marschner, 1991). Adaptations to alkaline conditions include pH decrease by excretion of protons to acidify the surrounding solution, reduction of Fe³⁺ to Fe²⁺ by Fe³⁺-chelate reductase, changes in root morphology, increase of citrate concentrations in the phloem and release of alkaline phosphatases (Römheld, 1991; Duff *et al.*, 1994; Guerinot, 2001; Hell & Stephan, 2003).

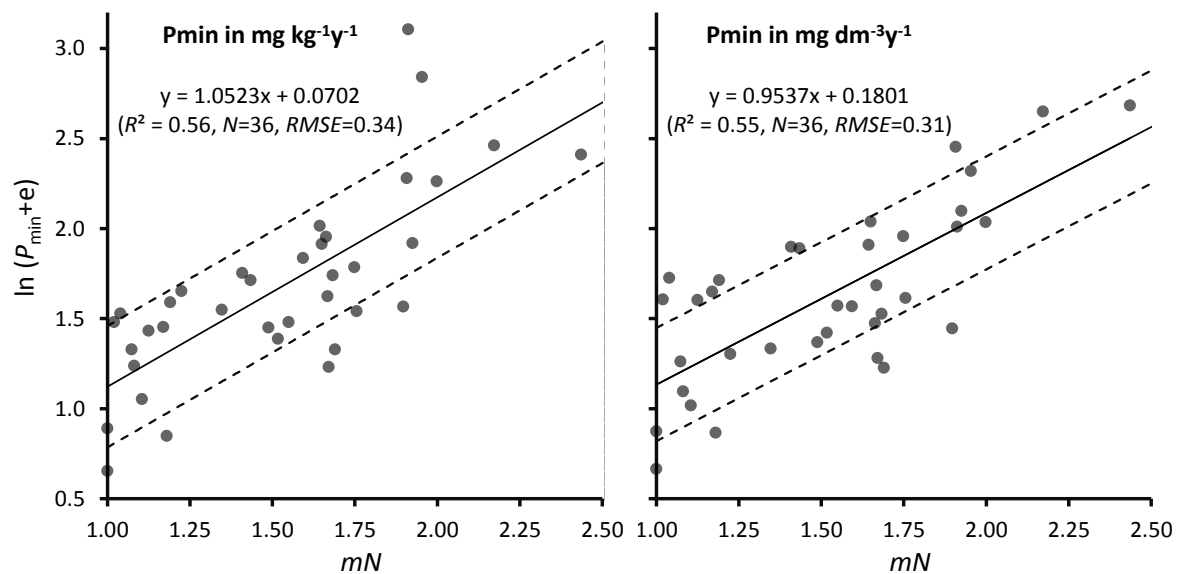


Figure 6. Relationship between average nutrient richness indication mN and phosphorus mineralization rate P_{\min} in the topsoil (0-10 cm), both on a mass basis (left) and on a volume basis (right) (+/- RMSE). Data from Fujita *et al.* (2013a).

Given the wide range of physiological adaptations of plants to pH controlled biogeochemical processes, soil pH can be seen as a good proxy for mR . On the basis of data collected by Staatsbosbeheer (Beets *et al.*, 2003), Cirkel *et al.* (2012) investigated relationships between soil pH (pH_{KCl}) measured in the topsoil (0-5 cm) and mR for terrestrial vegetation plots. He showed significant loss of relation in the weakly acid to alkaline range, for relevés indicating wet conditions. Probably this is caused by indifference for soil acidity of aerenchyma containing species. Plant species with shallow root systems, as adaptation to hypoxia, or mosses seem more responsive to soil acidity in wetland habitats and are probably better predictors of local soil pH. For predictions, it is thus important to differentiate between sites with and without severe oxygen stress. For this reason, we present pH- R_m relations for wet sites ($mF < 2.25$) and moist to dry sites ($mF \geq 2.25$) separately (Figure 7):

$$pH_{KCl}(0-5 \text{ cm}) = \begin{cases} 1.13 \exp(0.62mR) (N = 31, R_{adj}^2 = 45\%, RMSE = 1.17) & \text{if } mF < 2.25 \\ 1.19 \exp(0.63mR) (N = 58, R_{adj}^2 = 79\%, RMSE = 0.66) & \text{if } mF \geq 2.25 \end{cases} \quad [9]$$

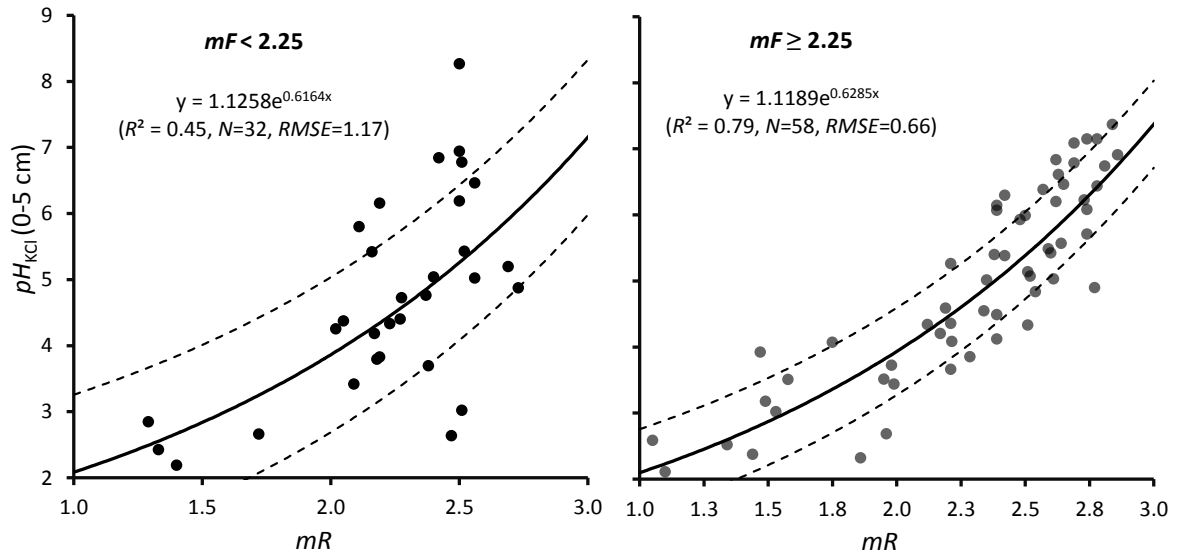


Figure 7. Relationship between average acidity indication mR_m and pH_{KCl} in the topsoil (0-5 cm) for wet sites (left) and moist to dry sites (right) (+/- RMSE). Data from Cirkel *et al.* (2014).

4 Concluding remarks

Results of provisional versions of ESTAR have been already been used in various studies, for instance to relate indicator values to environmental variables (Bartholomeus *et al.*, 2008a; Bartholomeus *et al.*, 2011a; Bartholomeus *et al.*, 2012; Fujita *et al.*, 2013a; Cirkel *et al.*, 2014), to classify vegetation types (Witte *et al.*, 2007; Douma *et al.*, 2012), to model vegetation response to water management and climate change (Witte *et al.*, 2004; Witte *et al.*, accepted; Van der Knaap *et al.*, submitted), and to map vegetation and habitat factors using remote sensing techniques (Roelofsen *et al.*, 2014; Roelofsen *et al.*, submitted).

We intend to regularly update ESTAR with new knowledge about the demands species make on their environment, and about relationships between plant characteristics (indicator values and functional traits *sensu* Pérez-Harguindeguy *et al.* (2013)) and physical factors (e.g. salinity). Updates will be made available through our website www.kwrwater.nl/watershare/home/ (search for 'sensing vegetation for soil and water').

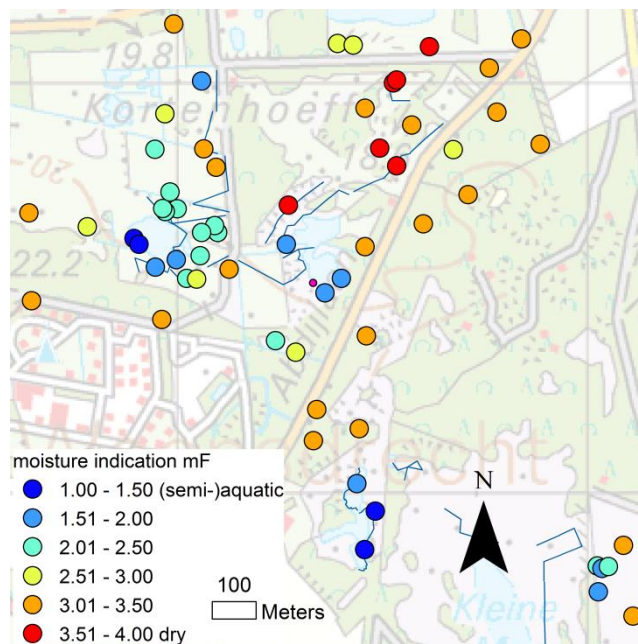


Figure 8. Average moisture indicator value mF of vegetation plots in nature reserve 'Brabantse wal'.

References

- Bartholomeus, R.P., Witte, J.P.M. & Runhaar, J. (2011a) Drought stress and vegetation characteristics on sites with different slopes and orientations. *Ecohydrology*, **5**, 808-818.
- Bartholomeus, R.P., Witte, J.P.M., Van Bodegom, P.M. & Aerts, R. (2008a) The need of data harmonization to derive robust empirical relationships between soil conditions and vegetation. *Journal of Vegetation Science*, **19**, 799-808.
- Bartholomeus, R.P., Witte, J.P.M., van Bodegom, P.M., van Dam, J.C. & Aerts, R. (2008b) Critical soil conditions for oxygen stress to plant roots: Substituting the Feddes-function by a process-based model. *Journal of Hydrology*, **360**, 147-165.
- Bartholomeus, R.P., Witte, J.P.M., Van Bodegom, P.M., Van Dam, J.C. & Aerts, R. (2011b) Climate change threatens endangered plant species by stronger and interacting water-related stresses. *J. Geophys. Res.*, **116**, G04023.
- Bartholomeus, R.P., Witte, J.P.M., Bodegom, P.M., Dam, J.C., Becker, P. & Aerts, R. (2012) Process-based proxy of oxygen stress surpasses indirect ones in predicting vegetation characteristics. *Ecohydrology*, **5**, 746-758.
- Beets, C.P., Hommel, P.W.F.M. & de Waal, R.W. (2003) *Selectie van referentiepunten t.b.v. het SBB-project terreincondities [Selection of reference points for the SBB terrain conditions project]*. Staatsbosbeheer, afdeling Terreinbeheer, Driebergen.
- Cirkel, D.G., Witte, J.P.M., Nijp, J.N., van Bodegom, P.M. & Zee, S.E.A.T.M. (2014) The influence of spatiotemporal variability and adaptations to hypoxia on empirical relationships between soil acidity and vegetation. *Ecohydrology*, **7**, 21-23.
- Clausman, P.H.M.A., Den Held, A.J., Jalink, L.M. & Runhaar, J. (1987) Het vegetatie-onderzoek van de provincie Zuid-Holland. Deelrapport 2: milieu-indicatie van vegetaties (Toewijs). In: Province of Zuid-Holland., The Hague (NL).
- De Jong, A. (1997) *Ijking van de vochttoestand van de bodem met de vochtindicatie van de vegetatie, volgens het ecotopensysteem [Calibration of the moisture conditions of the soil with the moisture indication of the vegetation according to the ecotope system]*. Landbouw Universiteit Wageningen, Wageningen.
- Dirkse, G.M. & Kruijsen, B.W.J.M. (1993) Indeling in ecologische groepen van Nederlandse blad- en levermossen. *Gorteria*, **19**, 1-29.
- Douma, J.C., Aerts, R., Witte, J.P.M., Bekker, R.M., Kunzmann, D., Metselaar, K. & Van Bodegom, P.M. (2012) A combination of functionally different plant traits provides a means to quantitatively predict a broad range of species assemblages in NW Europe. *Ecography*, **35**, 364-373.
- Duff, S.M.G., Sarath, G. & Plaxton, W.C. (1994) The role of acid phosphatases in plant phosphorus metabolism. *Physiologia Plantarum*, **90**, 791-800.
- Ellenberg, H. (1992) Zeigerwerte der Gefäßpflanzen (ohne *Rubus*). *Zeigerwerte von Pflanzen in Mitteleuropa* (ed. by H. Ellenberg, H.E. Weber, R. Düll, V. Wirth, W. Werner and D. Paulißen).
- Fujita, Y., Van Bodegom, P.M. & Witte, J.P.M. (2013a) Relationships between nutrient-related plant traits and combinations of soil N and P Fertility. *PLoS ONE* **8**(12), **8**, e83735.
- Fujita, Y., Van Bodegom, P.M., Runhaar, J., Olde Venterink, H. & Witte, J.P.M. (2013b) Towards a proper integration of hydrology in predicting soil nitrogen mineralization rates along natural moisture gradients. *Global Biogeochemical Cycles*, **58**, 302-312.
- Guerinot, M.L. (2001) Improving rice yields; ironing out the details. *Nat Biotech*, **19**, 417-418.
- Hell, R. & Stephan, U. (2003) Iron uptake, trafficking and homeostasis in plants. *Planta*, **216**, 541-551.
- Jansen, P.C. & Runhaar, J. (2005) *Toetsing van het verband tussen het aandeel xerofyten en de droogtestress onder verschillende omstandigheden [Testing of the relationship between*

- the covering of xerophytes and drought stress under different conditions*]. Alterra, Wageningen.
- Jansen, P.C., Runhaar, J., Witte, J.P.M. & Van Dam, J.C. (2000) Vochtindicatie van Grasvegetaties in Relatie tot de Vochttoestand van de Bodem [Moisture Indication of Grass Vegetations in Relation to the Moisture Conditions of the Soil]. *Alterra: Wageningen*, 65.
- Käfer, J. & Witte, J.P.M. (2004) Cover-weighted averaging of indicator values in vegetation analyses. *Journal of Vegetation Science*, **15**, 647-652.
- Klapp, H.C.E. (1965) *Grünlandvegetation und Standort nach Beispiel aus West-, Mittel- und Süddeutschland*. Paul Parey, Berlin/Hamburg.
- Londo, G. (1988) *Nederlandse freatofyten*. Pudoc, Wageningen.
- Marquardt, D.W. (1963) An algorithm for least-squares estimation of nonlinear parameters. *SIAM J. Appl. Math.*, **11**, 431-441.
- Marschner, H. (1991) Mechanisms of adaptation of plants to acid soils. *Plant and Soil*, **134**, 1-20.
- Mueller-Dombois, D. & Ellenberg, H. (1974) Aims and methods of vegetation ecology.
- Parton, W.J., Scurlock, J.M.O., Ojima, D., Gilmanov, T.G., Scholes, R.J., Schimel, D.S., Kirchner, T., Menaut, J.C., Seastedt, T., Garcia Moya, E., Kamnalrut, A. & Kinyamario, J.I. (1993) Observations and modeling of biomass and soil organic matter dynamics for the grassland biome worldwide. *Global Biogeochemical Cycles*, **7**, 785-809.
- Pérez-Harguindeguy, N., Díaz, S., Garnier, E., Lavorel, S., Poorter, H., Jaureguiberry, P., Bret-Harte, M.S., Cornwell, W.K., Craine, J.M., Gurvich, D.E., Urcelay, C., Veneklaas, E.J., Reich, P.B., Poorter, L., Wright, I.J., Ray, P., Enrico, L., Pausas, J.G., de Vos, A.C., Buchmann, N., Funes, G., Quétier, F., Hodgson, J.G., Thompson, K., Morgan, H.D., ter Steege, H., van der Heijden, M.G.A., Sack, L., Blonder, B., Poschlod, P., Vaieretti, M.V., Conti, G., Staver, A.C., Aquino, S. & Cornelissen, J.H.C. (2013) New handbook for standardised measurement of plant functional traits worldwide. *Australian Journal of Botany*, **61**, 167-234.
- Poozesh, V., Cruz, P., Choler, P. & Bertoni, G. (2007) Relationship between the AI Resistance of Grasses and their Adaptation to an Infertile Habitat. *Annals of Botany*, **99**, 947-954.
- Roelofsen, H.D., Kooistra, L., Van Bodegom, P.M., Verrelst, J. & Witte, J.P.M. (2014) Mapping a priori defined plant associations using remotely sensed vegetation characteristics. *Remote sensing of environment*, **140**, 639-651.
- Roelofsen, H.D., Van Bodegom, P.M., Kooistra, L., Van Amerongen, J.J. & Witte, J.P.M. (submitted) An evaluation of remote sensing derived site factors for use in ecological assessment studies. *Remote Sensing of Environment*,
- Römheld, V. (1991) The role of phytosiderophores in acquisition of iron and other micronutrients in graminaceous species: An ecological approach. *Plant and Soil*, **130**, 127-134.
- Runhaar, J. (1989) *Toetsing van het ecotopensysteem*. Rijksuniversiteit Leiden, Leiden.
- Runhaar, J. & Udo de Haes, H.A. (1994) Site factors as classification characteristics. *Ecosystem Classification for Environmental Management* (ed. by F. Klijn), pp. 139-172. Kluwer, Dordrecht/Boston/London.
- Runhaar, J., Witte, J.P.M. & Verburg, P. (1997) Ground-water level, moisture supply, and vegetation in the Netherlands. *Wetlands*, **17**, 528-538.
- Runhaar, J., van Landuyt, W., Groen, C.L.G., Weeda, E.J. & Verloove, F. (2004) Herziening van de indeling in ecologische soortengroepen voor Nederland en Vlaanderen [Revision of the classification in ecological species groups for the Netherlands and Flanders]. *Gorteria*, **30**, 12-26.
- Stevens, R.A.M., Runhaar, J., Udo de Haes, H.A. & Groen, C.L.G. (1987) Het CML-ecotopensysteem, een landelijke ecosysteemtypologie toegespitst op de vegetatie. *Landschap*, **4**, 135-149.
- Van der Knaap, Y.A.M., De Graaf, M., Van Ek, R., Witte, J.P.M., Bierkens, M.F.P. & Van Bodegom, P.M. (submitted) Potential impacts of groundwater conservation measures on catchment-wide vegetation patterns in a future climate. *Landscape Ecol.*,
- Van der Maarel, E. & Franklin, J. (2012) *Vegetation ecology*. John Wiley & Sons.
- Van Raam, J.C. & Maier, E.X. (1993) Overzicht van Nederlandse Kranswieren. *Gorteria*, **18**, 111-116.
- Witte, J.P.M. (1998) *National Water Management and the Value of Nature*. Wageningen Agricultural University, Wageningen.

- Witte, J.P.M. (2002) The descriptive capacity of ecological plant species groups. *Plant Ecology*, **162**, 199-213.
- Witte, J.P.M. & Van der Meijden, R. (2000) Mapping ecosystem types by means of ecological species groups. *Ecological engineering*, **16**, 143-152.
- Witte, J.P.M., Meuleman, J.A.M., Van der Schaaf, S. & Raterman, B. (2004) Eco-hydrology and biodiversity. *Unsaturated zone modelling: Progress, challenges and applications* (ed. by R.A. Feddes, G.H. De Rooij and J.C. Van Dam), pp. 301-329. Wageningen University and Research Centre, Wageningen.
- Witte, J.P.M., Wójcik, R.B., Torfs, P.J.J.F., De Haan, M.W.H. & Hennekens, S. (2007) Bayesian classification of vegetation types with Gaussian mixture density fitting to indicator values. *J. Veg. Sci.*, **18**, 605-612.
- Witte, J.P.M., Bartholomeus, R.P., Van Bodegom, P.M., Cirkel, D.G., Van Ek, R., Fujita, Y., Janssen, G., Spek, T.J. & Runhaar, J. (accepted) A probabilistic eco-hydrological model to predict the effects of climate change on natural vegetation at a regional scale. *Landscape Ecol.*,

Appendix: Ecological species groups and indicator values

An update of Appendix A of Witte et al. (2007)

The classification of ecotope types

The ecological species groups by Runhaar *et al.* (2004) make part of a classification of ecosystem types. The ecological species groups indicate which species are characteristic for these ecosystem types. The basic unit in the ecosystem classification is the ecotope, defined as: “a spatial unit that is homogenous in vegetation structure, stage of succession and in the dominant abiotic factors that determine the species composition of the vegetation” (Stevens *et al.*, 1987). Hence, from the biotic part of the ecosystem, only the vegetation is taken into account. As the vegetation is described in combination with its habitat, an ecotope is an ecosystem: an ecosystem of a certain size (small) and certain homogeneity (Runhaar & Udo de Haes, 1994).

For the classification of ecotope types, abiotic and biotic factors that determine the species composition of the vegetation have been used (Table 2). The main abiotic site factors (classification characteristics) of the ecotope system are Salinity, Moisture regime (characterizing the availability of both water and oxygen; Runhaar *et al.* (1997), Bartholomeus *et al.* (2012)), Nutrient availability and Acidity. Climate is also an important factor that influences the vegetation both directly (e.g. through frost) and indirectly (e.g. through soil development). However, it has not been used as a classification characteristic because within the Netherlands climate differences are small.

Vegetation structure was chosen as the main biotic classification characteristic. The vegetation structure is seen as a result of the operational factors ‘time’ (succession) and ‘vegetation management’ (Runhaar & Udo de Haes, 1994).

For each site factor several classes have been distinguished, each indicated by a symbol (Table 2). Subsequently, ecotope types have been constituted by combining classes, resulting in ecotope types such as G27: a grassland (G) on a wet (2), moderately nutrient-rich (7) site, or P42: a pioneer vegetation (P) on a moist (4) nutrient-poor and neutral (2) site. Not all the theoretically possible combinations of classes have been distinguished as ecotope types. Some combinations are ecologically less relevant. For example, in ecosystems that are very rich in nutrients, the influence of acidity on the species composition is far less pronounced than in nutrient-poor ecosystems (Figure 9). Therefore, in very nutrient-rich ecosystems acidity has not been used as a classification characteristic. In addition, many combinations of classes do not occur in the Netherlands (for instance the combination ‘woods and shrubs’ and ‘saline’).

Ecological species groups

The species composition of the ecotope types is described by means of ecological species groups. An ecological species group comprises plant species that are characteristic for a certain ecotope type. Species that occur in two or more ecotope types have been assigned to more than one ecological species group (up to a maximum of 10 groups). In this way the ecological amplitude of species is taken into account. By way of example Table 3 lists the ecological species groups of five vascular plant species, taken from Runhaar *et al.* (2004). The complete division of vascular plants into ecological groups is available at: www.synbiosys.alterra.nl/ecotopen.

Table 2. Classification characteristics and classification classes of the ecotope system (after Runhaar *et al.* (2004)). Ecotope types are constituted by combining classes. For instance P61 is a Pioneer vegetation (P) on a dry (6), nutrient-poor and acid (1) site.

Classification characteristic	Class (class code)
Salinity	fresh (0) brackish (b) Saline (z)
Vegetation structure	water vegetation (W) terrestrializing vegetation (V) pioneer vegetation (P) grassland vegetation (G) tall herbaceous vegetation (R)
Moisture regime	water (1) wet (2) moist (4) dry (6)
Nutrient availability + acidity	nutrient-poor + acid (1) nutrient-poor + weakly acid (2) nutrient-poor + alkaline (3) nutrient-poor (4) Moderately nutrient-rich + weakly acid (5) Moderately nutrient-rich + alkaline (6) Moderately nutrient-rich (7) very nutrient-rich (8)

The initial division into ecological groups has been based on expert judgment and on national and international literature, concerning for example indicator values of plant species (Klapp, 1965; Clausman *et al.*, 1987; Londo, 1988; Ellenberg, 1992). As a second step the consistency of the groups was tested using ca. 50,000 relevés from all over the Netherlands. These relevés served to check whether species attributed to a certain ecological group actually occur in combination with other species from the same group (Runhaar & Udo de Haes, 1994; Runhaar *et al.*, 2004). The reliability of the ecological groups has also been tested by comparing them with physical habitat factors measured in the field (Runhaar, 1989; Runhaar *et al.*, 1997; Bartholomeus *et al.*, 2011a; Bartholomeus *et al.*, 2012; Cirkel *et al.*, 2014) and by comparing maps of ecological groups with both ecological soil maps and vegetation maps (Witte, 1998; Witte & Van der Meijden, 2000; Witte, 2002; Witte *et al.*, 2007).

In the list with vascular plant species of Runhaar *et al.* (2004), the order in which the ecological groups is published for a species has an ecological meaning: the relative abundance of a species is largest in the ecotope type corresponding with the first species group, and smallest in the ecotope type corresponding with the species groups that is mentioned last. From Table 4 we can read that species

Table 3. Five records from the list of ecological species groups of Runhaar *et al.* (2004). No = species number.

No	Species name	Rank order species groups				
		1	2	3	4	5
940	<i>Pimpinella major</i>	G46				
941	<i>Pimpinella saxifraga</i>	G43	G47	G67	G63	G62
942	<i>Pinguicula vulgaris</i>	G22				
943	<i>Pinus sylvestris</i>	H61	H41	H62	H21	
944	<i>Plantago coronopus</i>	bP40				

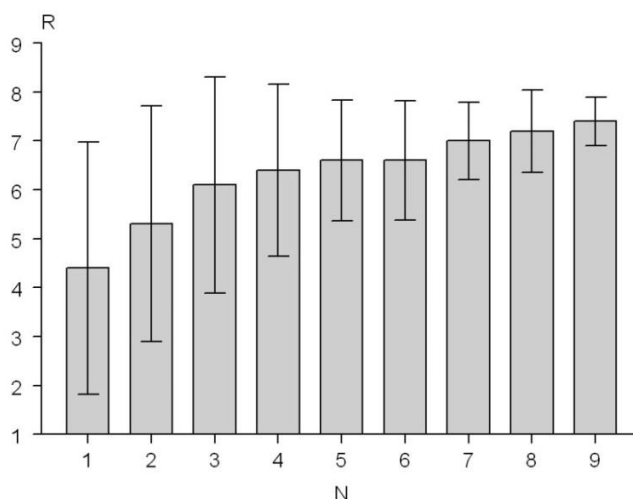


Figure 9. Relationship between indicator value for nutrient-availability N and average indicator value for acidity R (plus standard deviation). Constructed for Dutch vascular plant species on the basis of Ellenberg's list of indicator values Ellenberg (1992). From this result we concluded that nutrient-rich sites ($N > 6$) usually have a high indicator value for acidity.

assigned in five species groups the relative abundance in the ecotope type corresponding with the first ecological species group is, on the average, more than three times as high as in ecotope type represented by the fifth ecological species group (weight factors 0.353 and 0.112 respectively). The weight factors from Table 4 were used in the calculation of the indicator values per species. For instance, *Pimpinella saxifraga*, a species occurring in five ecological species groups (Table 3), is for 35.3% assigned to G43, for 22.5% to G47, for 17.3% to G67, for 13.7% to G63 and for the remaining 11.2% to G62.

Also lists of ecological species groups exist for mosses and liverworts (Dirkse & Kruijsen, 1993) and for *Characeae* (Van Raam & Maier, 1993). However, in these lists the order in which the groups are presented has no ecological meaning.

Indicator values of species

We first calculated how each species is divided among the various classes of the ecotope system. Consider for instance *Pimpinella saxifraga* again, and the weights of Table 3:

Species groups (Table 3): G43 G47 G67 G63 G62
 Weights (Table 4): 0.353 0.225 0.173 0.137 0.112

Table 4. Weights of ecological species groups in relation to the rank order in which a species was assigned to this group by Runhaar et al. (2004) and the number (#) of ecological groups assigned.

#	Rank order									
	1	2	3	4	5	6	7	8	9	10
1	1.000									
2	0.643	0.357								
3	0.500	0.295	0.205							
4	0.425	0.253	0.180	0.143						
5	0.353	0.225	0.173	0.137	0.112					
6	0.293	0.202	0.162	0.132	0.114	0.097				
7	0.281	0.186	0.146	0.118	0.102	0.089	0.079			
8	0.242	0.178	0.136	0.115	0.102	0.086	0.074	0.067		
9	0.223	0.161	0.132	0.111	0.095	0.081	0.073	0.065	0.059	
10	0.218	0.144	0.118	0.099	0.088	0.081	0.073	0.065	0.059	0.055

From this information it follows that *Pimpinella saxifraga* 'belongs to' moist sites (indicated by the first number 4 in the species group label) for a fraction of $f_{\text{moist}} = 0.353 + 0.225 = 0.578$ and to dry sites (indicated by the first number 6 in the species group label) for a fraction $f_{\text{dry}} = 0.173 + 0.137 + 0.112 = 0.422$. This computation of fractions was done for all species and also for the site factors Salinity, Nutrient availability and Acidity. The result is implemented in the file ESTAR.CSV. If, for a certain site factor, none of the fractions f was greater than 0.45, the species was considered to be indifferent to this site factor and, consequently, was omitted in the calculation of the indicator value. This rule resulted in the omission of only a few species (for instance, *Carex hirta* and *Salix repens* are the only omitted vascular species for the factor Moisture regime).

Since no similar weight factors were available for mosses, liverworts and *Characeae* (the order in which the groups are published has no ecological meaning for these taxa), the weight per ecological species group of these organisms was calculated as the inverse of the number of groups assigned to these species (Witte, 1998; Witte, 2002). So, if three groups were assigned to a species, each group got a weight of 0.333.

Next, the indicator value of species was calculated from the indicator values of the site factor classes. For moisture regime the indicator values for the classes are: water = 1, wet = 2, moist = 3, dry = 4. The moisture indicator value of for example *Pimpinella saxifraga* was calculated as the sum of the product of these figures and the moisture fractions: $1 \times 0.000 + 2 \times 0.000 + 3 \times 0.578 + 4 \times 0.432 = 3.42$. Or, to put it in general terms, the moisture value of a species, F , was calculated as:

$$F = 1f_{\text{water}} + 2f_{\text{wet}} + 3f_{\text{moist}} + 4f_{\text{dry}}$$

In a similar way, we calculated the indicator value for Salinity S :

$$S = 1f_{\text{fresh}} + 2f_{\text{brackish}} + 3f_{\text{saline}}$$

Example *Pimpinella saxifraga*: $F = 1 \times 0.000 + 2 \times 0.000 + 3 \times 0.578 + 4 \times 0.422 = 3.422$ and $S = 1 \times 1.000 + 2 \times 0.000 + 3 \times 0.000 = 1.000$.

In the current version of ESTAR, the weights W^v for both F and S ascribed to the indicator values of each species is always 1.0, except for the W^v of Peat moss species (*Sphagnopsida*) and Liverwort species (*Hepaticopsida*). Since species from these genera are very susceptible to the water regime, they were assigned an arbitrarily chosen higher weight of $W^v = 2.0$.

Since the ecotope system provides no information about the nutrient status of brackish and saline sites, we assumed that both saline and brackish sites are very nutrient-rich sites, but that for the brackish sites this rule is less reliable. To account for the uncertainty about the nutrient-richness of brackish sites, we introduced a factor g_b and computed N as:

$$N = \frac{1f_{\text{nutrient-poor}} + 2f_{\text{moderately rich}} + 3(f_{\text{very rich}} - (1 - g_b)f_{\text{brackish}})}{W^N}$$

where:

$$W^N = f_{\text{nutrient-poor}} + f_{\text{moderately rich}} + f_{\text{very rich}} - (1 - g_b)f_{\text{brackish}}$$

The factor g_b was set to 0.1, implying that $W^N < 1$ for species that are wholly or partly classified under brackish sites. Example *Plantago coronopus* (Table 3): $W^N = 0.000 + 0.000 + 1.000 - (1 - 0.1) \times 1.000 = 0.100$ and $N = 1 \times 0.000 + 2 \times 0.000 + 3 \times (1.000 - (1 - 0.1) \times 1.000) / 0.1 = 3.000$.

In the ecotope system, information about acidity is not provided for all ecological groups of very nutrient rich sites, nor for most ecological groups of moderately rich sites and some groups of nutrient poor sites. Examples are bR20, G28, G47 and G24. The code of such ecological groups ends with a figure for nutrient-availability and acidity of 0, 8, 7 and 4, respectively (Table 2). According to Figure 9, nutrient-rich sites on average have a high indicator value for acidity. Therefore, we assumed an average indicator value $R_u = 2.5$ for all ecological groups for which no information about acidity is given in the ecotope systems. Furthermore, applying a factor $g_u = 0.1$ we weighted ecological groups with known

acidity higher than groups with unknown acidity. This led to the following equation for the acidity indicator value R :

$$R = \frac{1f_{\text{acid}} + 2f_{\text{weakly acid}} + 3f_{\text{alkaline}} + R_u g_u f_u}{W^R}$$

where:

$$W^R = f_{\text{acid}} + f_{\text{weakly acid}} + f_{\text{alkaline}} + g_u f_u$$

$$f_u = 1 - (f_{\text{acid}} + f_{\text{weakly acid}} + f_{\text{alkaline}})$$

Example *Pimpinella saxifraga* (Table 3):

$$f_{\text{acid}} = 0.000, f_{\text{weakly acid}} = 0.122, f_{\text{alkaline}} = 0.353 + 0.137 = 0.490$$

$$f_u = 1 - (0.000 + 0.122 + 0.490) = 0.398$$

$$W^R = 0.000 + 0.122 + 0.490 + 0.1 \times 0.398 = 0.642$$

$$R = (1 \times 0.000 + 2 \times 0.122 + 3 \times 0.490 + 0.398 \times 0.1 \times 2.5) / 0.642 = 2.794.$$