



Eindrapportage-formulier TRIAS projecten
Final report format for TRIAS projects.

When a TRIAS project has finished, or is about to finish, a Final Report is required. This report serves several goals simultaneously:

- it enables the program commission to check whether the project has met its goals,
- it enables NWO-ALW to finalize the project administratively, e.g. pay the final part of the personnel costs of the project,
- it provides some of the information needed for evaluation purposes,
- it provides information which can be publicized, e.g. via a web site.

We have integrated the questionnaires from TRIAS and ALW into one, in order to prevent the need to fill in the same answers twice.

Please send in the filled out forms within a month after the project is completed to:

Netherlands Organisation for Scientific Research
Earth and Life Sciences
Carmen van Meerkerk and/or Theo Saat
P.O. Box 93510
2509 AM The Hague



Part I

General information, also intended for publication through the TRIAS website

01 Project title

Soils in transition: patterns and processes in soil ecosystems during the restoration of natural ecosystems on former agricultural land

02 TRIAS/ALW project number or file number

TRIAS project 835.80.011

03 Research period, at what date did the project start, at what date did it end

Subproject 1: Transition of soil life: shifts of fungal/bacterial ratios during the recovery of natural ecosystems 1st October 2002 – 31st January 2007

Subproject 2: Soil food web structure, soil ecosystem processes, and vegetation development, from 01-11-2002 to 30-10-2006.

Subproject 3 Food Web Modelling, from 1st June 2003 – 31st May 2007

04 Names of the researchers involved, the names and addresses of the institutes where the research work was carried out

Subproject 1:

PhD student Ir. Annemieke van der Wal (PhD student)
Netherlands Institute of Ecology (NIOO-KNAW)
Centre for Terrestrial Ecology
Department of Terrestrial Microbial Ecology
PO Box 40
6666 ZG, Heteren
The Netherlands

Supervisors: Dr. W. De Boer
Netherlands Institute of Ecology (NIOO-KNAW)
Centre for Terrestrial Ecology
Department of Terrestrial Microbial Ecology
PO Box 40
6666 ZG, Heteren
The Netherlands

Prof. Dr. J.A. van Veen
Netherlands Institute of Ecology (NIOO-KNAW)
Centre for Terrestrial Ecology

Department of Terrestrial Microbial Ecology
PO Box 40
6666 ZG, Heteren
The Netherlands

Subproject 2:

PhD student Drs. Paul Kardol
Netherlands Institute of Ecology (NIOO-KNAW)
Centre for Terrestrial Ecology
Department of Multitrophic Interactions
PO Box 40
6666 ZG, Heteren
The Netherlands

Supervisors: Prof.Dr.Ir. Wim H. van der Putten
Netherlands Institute of Ecology (NIOO-KNAW)
Centre for Terrestrial Ecology
Department of Multitrophic Interactions
PO Box 40
6666 ZG, Heteren
The Netherlands

Dr.Ir. T. Martijn Bezemer
Laboratory of Nematology
Wageningen University and Research Centre
PO Box 8123
6700 ES Wageningen
The Netherlands

Subproject 3:

PhD student Ir. Remko Holtkamp
Environmental Sciences
Copernicus Institute
Utrecht University
P.O.Box 80115
3508 TC Utrecht
The Netherlands

Supervisors: Dr. S.C. Dekker
Environmental Sciences
Copernicus Institute
Utrecht University
P.O.Box 80115
3508 TC Utrecht
The Netherlands

Prof. dr. P.C. De Ruiter
Soil Center
Wageningen University Research Center
Droevendaalsesteeg 4
6708 PB Wageningen
The Netherlands

05 Short scientific summary in English of: main research objective, research methods, results and conclusion

The restoration of former natural ecosystems on agricultural land is one of the major land conversion activities in industrialised countries. However, much is unknown about how soils respond to abandonment and how this influences ecosystem development. We disentangled the interplay between plant and soil communities by field surveys, experimental studies in the field, in the lab and greenhouse and modeling. The aim was to enhance our understanding of how soils respond to changing land use and how this response influences vegetation development and ecosystem functioning.

In a chronosequence of 26 ex-arable fields that had been abandoned 0-34 years ago, fungal biomass and the quality and quantity of the soil organic matter did not reach a level of a reference natural heathland ecosystem; nematode and plant communities did not develop in parallel and nematodes showed different successional diversity patterns than soil mites. Therefore, we conclude that development of plants are not indicative of soil organisms and that one group of soil organisms is not indicative of others.

Along the transition gradient, we found slow and unexpected changes in soil food web structure and C and N mineralization rate. This may be due to absence of a decrease in soil organic matter (SOM) quality, which was expected after land abandonment, but also to the high stability of the total soil food web as a whole. Moreover, the shift from a bacterial to a fungal energy channel in the soil food web proceeded slowly. Opportunistic fungi were responsible for the decomposition processes in ex-arable field and these fungi are stimulated by high quality organic matter, a large quantity of substrate and burial of the substrate into soil. With a dynamic model we show that a yearly low quality input to the soil organic matter makes fungi relatively more important in the decomposition process. Interestingly, total soil phosphorus declined with time since abandonment, which was not due to leaching. This is opposite to model estimates in previous studies and our results strongly suggest that dry sandy ex-arable soils are no source for phosphorus leaching when abandoned.

Soil organisms from recently abandoned fields speed up vegetation succession, whereas soil organisms from later succession stages slow down succession. Moreover, the early succession plants influence mid succession plant communities indirectly through changing soil community composition. These results originate from greenhouse experiments. In the field, effects of soil transplantation were less successful, probably due to poor survival of the soil organisms after transplantation. The application of soil transplantation, therefore, requires more detailed upscaling studies before being put into practice. Interestingly, in one ex-arable field heather (*Calluna vulgaris*) was able to become established right after abandonment and these plants had limited nitrogen mineralization due to ericoid mycorrhizal (ERM) fungi. This direct establishment of heather vegetation now needs to be tested in practice.

We conclude that the decomposer component of the soil food web develops slowly when compared to the herbivore, pathogen and symbiont component of the soil food web and the plant community development. Therefore, we conclude that on a short term, soil herbivores, pathogens and symbionts drive plant community development on ex-arable land, whereas on a longer term, the soil decomposer subsystem plays a more influential role.

06 Popular summary to inform the general public in Dutch

In Nederland is de afgelopen twee decennia ca. 100.000 ha landbouwgrond vrij gekomen voor natuurontwikkeling. Herstel van natuurlijke, soortenrijke heischrale graslanden (Nardo-Galion) en heide (Calluno-Genistion) zijn belangrijke doelen van natuurherstel. Het doel van het 'soils in transition' project was nagaan hoe het bodemvoedselweb reageert op uit productie name en hoe deze reactie de vegetatie-ontwikkeling en het functioneren van het ecosysteem beïnvloedt.

In een reeks voormalige landbouwvelden die overeenkomstig zijn in geschiedenis en omgevingsfactoren en tussen 0 tot 34 jaar geleden uit productie zijn genomen, nam de schimmelbiomassa nam alleen toe gedurende de eerste 2 jaar na het verlaten van de landbouwgrond. De hoeveelheid en kwaliteit van het organisch materiaal veranderde niet gedurende 34 jaar van uit productie name. De schimmelmenging bestond voor het belangrijkste deel uit snel groeiende schimmels en er waren weinig tot geen langzaam groeiende houtschimmels die gewoonlijk in bodems van natuurlijke ecosystemen voorkomen. In de oudere velden van de reeks nam zowel de biomassa van het schimmel- als het bacteriekanaal van het bodemvoedselweb toe en in het heideveld was de biomassa van het schimmelkanaal hoger dan de biomassa van het bacteriekanaal. De koolstof en stikstof mineralisatiesnelheden namen eerst toe en de stikstofmineralisatie nam weer af naarmate de landbouwgrond langer geleden uit productie was genomen. Dit kwam doordat door de hoge stabiliteit van het bodemvoedselweb, waardoor veranderingen in bodemontwikkeling slechts zeer langzaam verlopen na uit productie name.

Modelberekeningen laten zien dat bij jaarlijks toevoegen van moeilijk afbreekbaar organisch materiaal, wat door schimmels geprefereerd wordt, de schimmel tot bacterie verhouding zich sneller ontwikkelt richting de waarde die gemeten wordt in latere successiestadia. Het risico van het uitspoelen van fosfaat na het uit productie nemen van landbouwbodems is gering en spoelt niet uit naar diepere grondlagen.

In de reeks van uit productie genomen landbouwgronden was de ontwikkeling van de vegetatie niet indicatief voor de ontwikkeling van de nematodengemeenschap, terwijl de nematoden en mijten verschillende ontwikkelingspatronen volgden. Terwijl de vegetatie zich tot heideschraalland ontwikkelde, ging de nematodengemeenschap meer op die van een heideveld lijken. Voor de beoordeling van bodemdiversiteit gedurende een successiegradiënt en in natuurherstelprojecten is het van groot belang op welke schaal wordt gemeten en welke groep van bodemorganismen hiervoor als indicator wordt gebruikt.

In vroege successie-stadia versnelt een negatieve terugkoppeling – wellicht veroorzaakt door opbouw van bodemziekten – de vervanging van onkruiden door later-successie graslandsoorten. In latere successiestadia bestaat er een positieve terugkoppeling (wellicht veroorzaakt doordat symbiotische schimmels) waardoor de vegetatie-successie wordt vertraagd. De positieve terugkoppeling kan bijdragen aan een hogere diversiteit en stabiliteit van het systeem.

Op een voormalig landbouwveld waarvan de nutriëntrijke bovenlaag is verwijderd had het uitstrooien van maaisel uit een natuurgebied het grootste effect op de vegetatie-ontwikkeling. Het uitstrooien van grond uit een natuurgebied had een gematigd positief effect, maar het inbrengen van plaggen was niet erg succesvol. Verder onderzoek dient uit te wijzen hoe de overleving van soorten in de plaggen kan worden bevorderd. Het inbrengen van stro- en houtsubstraten in een niet-afgegraven landbouwgrond had weinig effect op de vegetatie-ontwikkeling. Op de droge zandgronden wordt de vegetatiesuccessie geremd door zaadlimitatie en niet door de nutriëntenstatus van de bodem.

Heideplanten (*Calluna vulgaris*) konden zich in goed vestigen en handhaven op een ex-landbouwbodem als ze zich konden vestigen voor de snelgroeiende planten. De ericoïde mycorrhizaschimmels gaven de heideplanten een betere toegang tot stikstof ten opzichte van de grassen en kruiden. Deze resultaten suggereren dat heide direct hersteld kan worden op ex-landbouwterreinen en dienen in een opschalingsexperiment in de praktijk te worden getoetst.

Conclusie: de ontwikkeling van de bodem organische stof, de bodemgemeenschap en het bodemvoedselweb op voormalige landbouwgronden in de richting van een heideveld verloopt zeer langzaam in vergelijking met het ontwikkeling van de plantengemeenschap. Op korte termijn spelen bodemziekten, wortelherbivoren and symbionten een belangrijkere rol in vegetatie-ontwikkeling. Vegetatie-ontwikkeling is een matige indicator voor de ontwikkeling van de bodemgemeenschap.

07 What impact and relevance has this project's outcome for practicing soil protection and/or soil remediation?

- *Calluna*-plants in ex-arable fields can establish themselves between ruderal plants if there is a seed inoculum available immediately after land abandonment, as well as the presence of the ericoid mycorrhizal symbiont. This practice needs to be scaled up, by examining how to establish *Calluna*.
- The development of species-rich grasslands / heath lands on ex-agricultural fields can be more easily influenced by spreading hay than by spreading soil from nature reserves.
- Phosphorous is not leaching into deeper soil layers.
- The saprotrophic fungal biomass can be enhanced after applying an organic layer to the soil.
- The assessment of the success of biodiversity restoration and ecosystem development on ex-arable land cannot be assessed only by quantifying aboveground diversity estimates.
- Successional changes in soil communities depend on the spatio-temporal scale and the groups of organisms considered.
- On small temporal and spatial scales, successional replacements in plant communities can strongly depend on interactions with soil communities.
- Adding substantial yearly amounts of organic matter to the field can cause a faster shift from a bacterial dominated towards a fungal dominated soil food web.

08 Please list the presentations held in connection to this project

Subproject 1:

Oral presentations Annemieke van der Wal

Spontaneous establishment of *Calluna vulgaris* on ex-arable soil: role of ericoid mycorrhizal fungi. Meeting functional biodiversity INRA, Champenoux (France), November 2006.

Spontaneous establishment of *Calluna vulgaris* on ex-arable soil: role of ericoid mycorrhizal fungi. Najaarsvergadering Sectie mycology, November 2006.

Spontaneous establishment of *Calluna vulgaris* on ex-arable soil: role of ericoid mycorrhizal fungi. Working-group soil microbiology and soil pathogens, November 2006.

The role of soil micro-organisms during restoration of arable land, Lecture 'functional biodiversity', Wageningen University, October 2006.

The role of ericoid mycorrhizas during natural colonization of *Calluna* in former agricultural land. Symposium 'Soil & Water', Zeist, Juni 2006

Fungal biomass development in former agricultural land. NIOO Days, Lunteren, March 2005.

Fungal development in secondary succession. PhD Verweij days, Texel, February 2005.

Soils in transition: Development of fungal biomass in ex-agricultural land. Symposium 'Soil & Water', Zeist, June 2004.

Development of fungal biomass in ex-agricultural land. Meeting DLG, Utrecht, March 2004.

Poster presentations Annemieke van der Wal

Possible mechanism of spontaneous establishment of *Calluna vulgaris* in a recently abandoned agricultural field. Congres 'International Symposium Microbial Ecology', Vienna (Austria), August 2006.

Development of fungal decomposition functions in former arable land. IOBC meeting 'Multitrophic interactions in soil', Wageningen University, June 2005.

Development of fungal decomposition functions in former arable land. Symposium 'Soil & Water', Zeist, June 2005.

Development of fungal biomass in ex-agricultural land. Congres 'Microbial planet: sub-surface to space', Cancun (Mexico), August 2004.

Transition of soil life: shifts of fungal/bacterial ratios during the recovery of natural ecosystems. Symposium 'Bodemdiep', Zeist, June 2003.

Transition of soil life: shifts of fungal/bacterial ratios during the recovery of natural ecosystems. Annual Symposium of the British Ecological Society 'Biological Diversity and Function in Soils', Lancaster University (UK), March 2003.

Transition of soil life: shifts of fungal/bacterial ratios during the recovery of natural ecosystems. PhD Verweij days, Texel, January 2003.

Transition of soil life: shifts of fungal/bacterial ratios during the recovery of natural ecosystems. NIOO Days, January 2003.

Subproject 2:

Oral presentations Paul Kardol

Functional biodiversity and ecosystem restoration. Lecture 'Functional Biodiversity', Wageningen University, October 2006

Microbe-mediated plant-soil feedback in pioneer stages of secondary succession causes long-lasting historical contingency effects in plant community composition. 91th Annual Meeting ESA, Memphis (USA), August 2006.

Land-use changes: interactions between plant and soil community development. National workshop 'Opportunities in Global Change Research', Amsterdam, February 2006.

Besides plants, soil organisms provide added value as indicators for conservation and restoration success. XVII International Botanical Congress, Vienna (Austria), July 2005.

The role of soil organisms in secondary succession and their value as indicators for conservation and restoration success. 35th Annual Conference GfÖ, Regensburg (Germany), September 2005.

The role of soil organisms in secondary succession and their value as indicators for conservation and restoration success. Annual Meeting British Ecological Society (BES), Hertfordshire (UK), September 2005.

Successional trajectories of soil nematode and plant communities in a chronosequence of ex-arable lands. Symposium Soil & Water, Zeist, June 2005.

Correlation and discrepancies between soil nematode and plant community development during secondary succession. GfÖ Workshop on Restoration Ecology, Giessen (D), April 2005.

Correlation and discrepancies between soil nematode and plant community development during secondary succession on ex-arable land. NIOO Days, Lunteren, March 2005.

Vegetation succession and soil nematode community development after land abandonment. PhD Verweij days, Texel, January 2005.

Soils in transition: above- and belowground development during secondary succession. PhD Verweij days, Texel, January 2004.

Poster presentations Paul Kardol

Restoration of ex-agricultural land: vegetation succession and changes in the soil food web. IOBC-meeting 'Multitrophic Interactions in soil', Wageningen, June 2005.

Restoration of ex-agricultural land: vegetation succession and changes in the soil food web. XIVth International Colloquium on Soil Zoology and Ecology, Rouen (F), September 2004.

Soils in transition: above- and belowground development. XXVIIth ESN International Symposium, Rome (I), June 2004.

Soils in transition: above- and belowground development. Symposium Soil & Water, Zeist, June 2004.

Soils in transition: soil food web structure, soil ecosystem processes and vegetation development in secondary succession. BES symposium 'Soil Biodiversity and Function', University of Lancaster (UK), March 2003.

Soils in transition: soil food web structure, soil ecosystem processes and vegetation development in secondary succession. Symposium Bodemdiep, Zeist, June 2003.

Soils in transition: soil food web structure, soil ecosystem processes and vegetation development in secondary succession. PhD Verweij days, Texel, January 2003.

Subproject 3:

Oral presentations Remko Holtkamp

Information indices as a tool for quantifying successional development of ecosystems. Ecosystem Networks Workshop, Copenhagen (Denmark), June 2006.

Dynamics of the soil food web structure during the transition of Agricultural to natural ecosystems. Symposium Soil & Water, Zeist, June 2006.

Soils in transition: modelling patterns and processes in soil ecosystems during the restoration of natural ecosystems on former agricultural land. Symposium Soil & Water, Zeist, June 2005.

Soils in transition: modelling patterns and soil of former agricultural ecosystems. NVTB (Nederlandse vereniging voor theoretische biologie) dagen, Schoorl, March 2005.

Poster presentations Remko Holtkamp

Soils in transition: modelling patterns and processes in soil ecosystems during the restoration of natural ecosystems on former agricultural land. Symposium Soil & Water, Zeist, June 2004.

Soils in transition: modelling patterns and processes in soil ecosystems during the restoration of natural ecosystems on former agricultural land. Symposium BodemDiep, Zeist, June 2003.

Soils in transition: modelling patterns and processes in soil ecosystems during the restoration of natural ecosystems on former agricultural land. Copernicus Heidagen, Den Haag, November 2003.

09 Please list publications in connection to this project

Publications in refereed journals

Kardol, P., T. M. Bezemer and W.H. van der Putten. Complementary effects of soil organism and plant propagule introductions in restoration of species-rich grassland communities. Accepted by Restoration Ecology.

Van der Wal, A., J.A. van Veen, W. de Boer et al. Possible mechanism of spontaneous establishment of *Calluna vulgaris* in a recently abandoned agricultural field. Accepted by Restoration Ecology.

Van der Wal, A., W. de Boer, I. M. Lubbers and J. A. van Veen. Concentration and vertical distribution of total soil phosphorus in relation to time of abandonment of arable fields. Accepted by Nutrient Cycling in Agro-ecosystems.

Holtkamp, R. and M.A. Tobor-Kaplon (in press). Information indices as a tool for quantifying development of belowground terrestrial ecosystems. Ecological modeling.

Tobor-Kaplon, M.A., R. Holtkamp, U.M. Scharler, A. Doroszuk, F.J.A. Kuenen, J. Bloem and P.C. de Ruiter (in press). Can information indices (Ecosystem Network Analysis) be used as indicators of environmental stress in terrestrial ecosystems? Ecological Modeling.

Kardol, P., N.J. Cornips, M.M.L. van Kempen, J.M.T. Bakx-Schotman and W.H. van der Putten (2007) Micro-mediated plant-soil feedback in pioneer stages of secondary succession causes long-lasting historical contingency effects in plant community composition. Ecological Monographs 77: 147-162.

Van der Wal, A., J. A. van Veen, W. Smant, H. T. S. Boschker, J. Bloem, P. Kardol, W. H. van der Putten, and W. de Boer. 2006. Fungal biomass development in a chronosequence of land abandonment. Soil Biology & Biochemistry 38:51-60.

Kardol, P., T.M. Bezemer and W.H. van der Putten (2006). Temporal variation in plant-soil feedback controls succession. Ecology Letters 9: 1080-1088.

Van der Wal, A., J. A. van Veen, A.S. Pijl, R.C. Summerbell, and W. de Boer. 2006. Constraints on development of fungal biomass and decomposition processes during restoration of arable sandy soils. *Soil Biology & Biochemistry* 38: 2890-2902.

De Ridder – Duine, A.S., Smant, W., Van der Wal, A., Van Veen., J.A., De Boer, W. 2006. Evaluation of a simple, non-alkaline extraction protocol to quantify soil ergosterol. *Pedobiologia* 50: 293-300

Kardol, P., T.M. Bezemer, A. van der Wal and W.H. van der Putten (2005). Successional trajectories of soil nematode and plant communities in a chronosequence of ex-arable land. *Biological Conservation* 126: 317-327.

Manuscript submitted

Holtkamp, R., A. van der Wal, P. Kardol et.al. Soil food web dynamics in ecosystem development after land abandonment. Submitted to *Applied Soil Ecology*.

Kardol, P., A. van der Wal et al. Seed addition outweighs soil fertility reduction measures in plant community development during ecosystem restoration on ex-arable land. Submitted to *Journal of Applied Ecology*.

Book chapters

De Boer, W. and van der Wal, A. 2007. Interactions between saprotrophic basidiomycetes and bacteria. In : *Ecology of Saprotrophic Basidiomycetes* (L. Boddy, J.C. Frankland & P.C. van West, eds.). *British Mycological Societal Symposium Series*, Elseviers (in press.)

Kulmatiski, A and P. Kardol. Getting plant-soil feedback out of the greenhouse: experimental and conceptual approaches. *Progress in Botany* 69.

Manuscripts in preparation

Van der Wal, W. de Boer, J. A. van Veen et al. Influence of environmental factors, N-addition and substrate accessibility on the initial stage of wood decay.

Kardol, P., J.S. Newton, T. M. Bezemer, M. Maraun, A. van der Wal and W. H. van der Putten. Diversity patterns and community development of soil mites and nematodes in secondary grassland succession.

Holtkamp, R., A. van der Wal, A., P. Kardol, S.C. Dekker and P.C. de Ruiter. The effect of soil food web structure on mineralization rates during ecosystem development

Holtkamp, R., S.C. Dekker and P.C. de Ruiter. Plant input to soil organic matter in relation to fungal and bacterial dynamics after land abandonment.

10 Please list Patent applications or other professional products (including contracts, articles in the popular media, contributions to documentaries or scientific television or radio programs, CD-ROMS, DVD or other (electronic) media).

None



Part II

Detailed information, primarily intended for administrative and statistical use by NWO-ALW

11a Under item 5 you have filled in the main research objectives. Please list all the original research objectives as indicated in the project's application and both indicate as well as motivate, to what extent these goals were realised, and/or whether the original research objectives had to be adapted.

Original objectives subproject 1:

1) To provide an estimate of the duration of conversion of a bacterial dominated decomposer system into a mixed decomposer system.

This objective is realized in the first study, where we analyzed the development of the fungal and bacterial biomass along a chronosequence of abandoned arable fields.

2) To examine which consequences conversion of a bacterial-dominated decomposer system into a mixed one has on the dynamics of protozoa.

This objective is realized in subproject 1, 2 and 3 together. We (PhD students from subproject 1, 2 and 3) analyzed the dynamics of the soil food web in 4 different fields, 3 ex-arable fields and one heathland. Protozoa were included in this study, and the final manuscript is written by Remko Holtkamp (subproject 3).

3) To indicate the consequences of delay of fungal colonization for nutrient retention.

This objective is realized in studies where we added different carbon substrates to different soils. We measured the nitrogen immobilization and the bacterial and fungal biomass in these studies.

4) To indicate the constraints for fungal colonization of abandoned agricultural fields.

This objective was also realized in the carbon addition studied. We found that fungal biomass could be increased after addition of carbon. We also observed in the chronosequence study that fungal biomass could increase during the first two years after abandonment of arable fields, indicating that disturbance by tillage is also an important constraint for an increase in fungal biomass.

5) To provide practical measures for enhancing the colonization of abandoned agricultural field by fungi.

This objective is realized in a field experiment in collaboration with subproject 2 and 3. In a recently abandoned field, we added straw and birch wood, as well as seeds to improve the development into a more natural ecosystem. We investigated if we could enhance immobilization of nutrients into microbial biomass by addition of carbon sources and if this could improve the vegetation development. The other aim was to determine if vegetation development is limited by the presence of wanted seeds. Paul Kardol (subproject 2) has written the manuscript.

Original objective subproject 2:

1) Analyse the relationship between the plant community structure (plant species diversity, early vs. mid succession plant species) on the nematode community structure.

Realised: we analysed the relationship between vegetation development and soil nematode community development (both taxonomically and functionally) in a chronosequence study (26 ex-arable fields, 3 current arable fields and 3 reference sites).

2) Examine the relation between vegetation development, food web complexity, food web processes, and the strength of the natural top-down control of root pathogens and root herbivores.

We examined the relationship between vegetation development and the strength of natural top-down control in greenhouse plant-soil feedback experiments. The experimental set-up did not allow us to examine the relationship between vegetation development and food web complexity and food web processes.

3) Analyse the effects of initial ecosystem development (introducing of plants, soil organisms, top soil removal) on resistance and resilience of the plant communities and ecosystem processes against stress (i.c. summer drought).

This experiment was cancelled and replaced by greenhouse experiments to study soil legacy effects.

Original objectives subproject 3:

1) Relate explicitly (changes in) population (dynamics) to (changes in) the (dynamics of) ecosystem processes, such as mineralisation, by using the food web energy flow model.

We studied the effect of the soil food web structure on C and N mineralisation rates by calculating contributions of particular groups of organisms to the mineralisation rates. Moreover, we calculated these contributions for different stages in transition so that differences in soil food web can be related to the flows.

2) Analyse the effects of environmental change on the stability of soil food webs with the food web stability model. Moreover, in combination with the food web energy flow model, it is also possible to analyse the effects of environmental change on the stability of ecosystem processes.

We calculated soil food web stability with the model on four different fields with different time since land abandonment. Stability of the soil food web appeared to be very high, also in contrast to previously published webs. Because of this high stability changes in soil food web structure will be low. We also showed that the fungal energy channel stability was higher than soil food web stability and stability of other energy channels. Therefore, we concluded that the fungal channel enhances stability.

3) Quantify the successional stage of the various fields with Trophic Network Analysis.

M.A. Tobor-Kaplon (see also cooperation section) and myself evaluated the usefulness of network analysis for quantifying soil succession. Results suggest that some indices of the network analysis showed can be used in this perspective. Quantification of ecosystem development after land abandonment showed that there was a difference in maturity between the ex-arable fields: the youngest soil was less mature than the other two ex-arable soils. Results also indicate that the heathland is slightly more mature than the oldest ex-arable field. Finally, results indicate that the development on ex-arable was in the direction of that of a heathland.

11b Did the project also include objectives which were not scientific? For instance, did the project also intend to apply research results, or strengthen the economic position of certain businesses?

Our field experiments provide applicable results for nature restoration practices on ex-arable fields.

11c Did the project's aims include the expanding the (international) network of contacts (at what level), providing education, improve communication, serve as input for policy drafting or policy decisions, etc.? Please motivate.

Subproject 1:

We closely collaborated with Dr. Jaap Bloem, Wageningen University, Dr. Boschker, NIOO-CEME and Dr. Summerbell, CBS. They helped us with their expertise to improve our manuscripts.

Subproject 2:

We closely collaborated with Dr. Mark Maraun (mites), TU Darmstadt (Germany) and we interacted with Dr. Matty Berg at VU Amsterdam.

Subproject 3:

We closely worked together with Dr. Michael Bonkowski, TU Darmstadt (Germany) to learn the method for protozoa biomass measurements and with Dr. Ursula Scharler, University of KwaZulu, Durban, (South Africa) for using the network analysis for soil ecosystems.

12 Do the results obtained match the original objectives? Please provide a short motivation why they do or don't.

Yes, they do. We analysed major changes in the soil community in relation to major soil processes as affected by the conversion of high input-output agricultural to a low input-output natural soil. We also examined which patterns and processes in the soil compartment are critical to the restoration of species-rich target vegetation. Subproject 3 is now analysing the stability of the major soil processes and we have already actively disseminated results, via SKB, end users, and scientific journals. Currently, the last papers are being prepared and we also will write papers in Dutch for end users and stake holders journals.

13 Will the results of this project serve as input for an initiative integrating/and or generalizing input from several projects, for instance into a (numerical) model, or into more understanding at the higher/system level? If so, was this intended and optimised from the beginning or did it occur by chance/ spontaneous? Please elaborate.

The measurements of the soil food web, including all soil organisms, roots and soil organic matter, were used to parameterize the model to calculate nutrient fluxes in the soil. These fluxes, in turn, are used for stability analysis and network analysis (see subproject 3 aims) in order to relate soil food web structure and soil processes to food web stability.

14 To what extent has this research project pointed the way in which further research has to be undertaken? Please motivate the guiding role perceived.

Our results showed that what you find in pot experiments do not necessarily have to match with the situation in the field. For example, we added carbon to soil in a pot experiment and observed that fungal biomass is enhanced after this addition. However, when we applied carbon in the field, we could not find any increase in fungal biomass. Probably, fungi are colonizing the wood fragments itself and do not explore their surroundings as much as we thought. This is expressing the necessity to always combine a pot experiment with a field experiment.

Furthermore, we showed that ericoid mycorrhizal fungi and the time of colonization are important factors during the successful establishment of *Calluna* plants on ex-arable soils. We observed this in the field, however, we did not test this experimentally, so it would be wise to first test our hypothesis before it is used in restoration management.

The results from this project strongly emphasize the importance of combining greenhouse and field experiments: there may be a large gap between mechanisms that potentially play a role in plant-soil interactions (greenhouse results) and the relative importance of these mechanisms in a field situation (field results). Also, our results stress the importance of considering the appropriate spatial and temporal scales in plant-soil studies

15 In what way, and to what extent, are the results reached of importance to research done by others? Please motivate or elaborate.

Our results are of interest for researchers that are interested in general ecological mechanisms, such as plant-soil interactions, microbe-plant interactions and soil processes as nutrient cycling and decomposition performed by micro-organisms that apply different life strategies. Moreover, this is of interest for both empiricalists and modellers as we used both approaches. Furthermore, our results are also important for nature managers and policy makers that are interested in restoration of degraded ecosystems. We also tested theoretical concept concerning succession, community assembly and diversity, which all are 'hot topics' in current and future ecological research.

16 Are you aware of any essential gaps or obstacles standing in the way of applying the results from your research project? Please elaborate.

One obstacle may be that we find that it is important to inoculate the field with seeds of target plants just after abandonment. Some nature managers told us that it is not allowed to inoculate seeds in nature, since nature management is than more referred to as gardening. However, this obstacle may be overcome by the addition of soil (with wanted seeds) of a natural ecosystem.



Part II - continued

Detailed information, primarily intended for administrative and statistical use by NWO-ALW

17 Which new research questions were generated through this project?

New research questions include:

Is an increased fungal biomass indeed contributing to carbon sequestration and nutrient retention?

Is increased saprotrophic fungal biomass counteracting the negative influence of plant pathogens and how will this effect the plant composition?

Furthermore, we found that the size of the substrate is influencing the microbial diversity. It is of interest to investigate factors that influence microbial diversity and to assess what these effects are on soil ecosystem functioning.

Another major question that was generated through this project concerns spatio-temporal scales and effects of assembly history on (plant) community composition:

- On what spatio-temporal scales do direct and indirect biotic plant-soil feedback and legacies operate?
- Does assembly history affect spatio-temporal plant community interactions (facilitation / inhibition; native / exotic species) through biotic plant-soil feedback and legacies?
- Are biotic plant-soil feedback and legacies effects on plant community composition historically contingent and do they explain large scale spatio-temporal vegetation patterns?
- Can field scale patterns of plant invasions be attributed to biotic plant-soil feedback and legacies?

Finally, it also may be of high interest to test importance of soil community development in plant community dynamic relative to aboveground processes, such as grazing of large herbivores or activity of wild boars.

18 In what way did you link this project to other projects within the TRIAS-program or link it to projects outside TRIAS? Did you cooperate within the TRIAS-program and did this cooperation lead to integrated results?

We cooperated with TRIAS project 835.08.008 Ecosystem Stability Analysis (ESA): towards a quantitative guide for user oriented soil management and ecological soil quality assessment. Remko Holtkamp (as part of subproject 3) has written two manuscripts together with Maria Tobor-Kaplon (Trias project 835.80.083).

19 Can you elaborate on the impact on society as a whole of your results (e.g. societal organisations, NGO's, businesses, schools, municipal authorities, etc.)

Our results will be of high interest to NGO's, such as nature conservation and land management organisations in The Netherlands, Natuurmonumenten and Staatsbosbeheer, as well as the Land Management Agency DLG, because of the applicability for nature restoration on ex-arable land, which to date is a common practice in the Netherlands.

20 What actions were taken to disseminate the results in the direction of the general public, besides the usual scientific channels?

We have planned to write some articles for semi-scientific journals, such as de Boerderij, De Levende Natuur and Bodem. We presented our results during meetings with officers from DLG and VROM and to the society of Bodembreed.

21 Have the researchers involved obtained a new position or employment after the project came to an end? Please specify and elaborate!

Annemieke van der Wal (subproject) one obtained a position at the RIVM as 'Researcher Soil Quality'. Paul Kardol has been offered a position in Knoxville/Oakridge Tennessee, USA in the OCCAM project (<http://warming.ornl.gov/OCCAM/>).

Heteren, June 25, 2007.