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Using nurse species as a potential nature-based solution for restoring herbaceous plant communities and soils in abandoned quarries in Lebanon : results from ex-situ mesocosm experiments

Houssam Shaiban

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Institut Méditerranéen de Biodiversité et d'Ecologie

Présentée par
Houssam SHAIBAN

Using nurse species as a potential nature-based solution for restoring herbaceous plant communities and soils in abandoned quarries in Lebanon: results from ex-situ mesocosm experiments.

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“You cannot get through a single day without having an impact on the world around you. What you do makes a difference, and you have to decide what kind of difference you want to make.”

Dr. Jane Goodall

Foreword

This thesis was achieved within the Mediterranean Institute of Biodiversity (IMBE) and the National Council for Scientific Research- Lebanon (CNRS-L). It was co-directed by Thierry Dutoit (CNRS Research Director - France) and Carla Khater (CNRS-L Research Director - Lebanon). The work has been financed by Avignon University, CNRS France, and IRD, and was part of the two projects 'TREET' and 'RESTORE', funded by Grant Research Program- CNRS Lebanon and CEDRE program. Furthermore, the work was funded by AUF (*Agence Universitaire de la Francophonie*) for the years 2017 to 2019. Also, it was supported by the LIA O-LiFE contribution (number SA 41-2018).

This manuscript includes a general introductory section that permits situating the work within a broader research problem and presents the framework, objectives, questions, and hypotheses of the thesis. It consists of an extensive literature review of the ecological difficulties of the semiarid Mediterranean environment and the status of quarries in Lebanon. The second section encompasses the methodological approach used to perform the research, followed by three-body chapters, a discussion section, and finally, a bibliography section amassing all cited references.

The first article (chapter 1) has been published in the *Lebanese Science Journal* (Volume 22, No. 1, 2021). The second article (chapter 2) is currently in preparation for the journal *Ecological Engineering*, whereas the third article (chapter 3) is in preparation for the journal *Applied Vegetation Science*.

The form of this manuscript necessitates some minor repetitions, particularly between the "General Introduction" section and some sections of the second and third papers.

Acknowledgment

In 2014, within the span of a few months, The Islamic State of Iraq and Syria (ISIS) mercenaries seized control over major territories in Iraq and Syria. Both countries, part of an ever-turmoiled cursed Middle East region and adjacent to Lebanon, are at least 20 to 30 times the size of Lebanon, my homeland. Fear of the unknown gripped us one afternoon as we watched the live streaming of the ISIS mercenaries descending the Syrian border mountain into Lebanon. At that moment, we knew that we needed a plan B- at least for our psychological ease. Dolly, my significant half, decided to pursue a long-dropped dream of studying Psychology and she is now finalizing her graduate thesis and completing her training. Whereas I thought of doing a Ph.D., since, at the time, we thought that it could open a door abroad, should we ever need to flee the country with our two boys, aged 3 and 6 at the time.

Fast-forward to the year 2022, ISIS deteriorated into an almost forgotten nightmare, whereas my Ph.D. materialized into reality. The five years, from 2017 to 2022, during which I was working on the doctoral thesis, all hell broke loose. The 2014 ISIS threat was, followed by social unrest and agitations throughout the country, culminating in the October 2019 revolution, infamous Beirut port blast in 2020, destroyed almost half of the capital – I was in the vicinity of the blast area then and miraculously survived. This catastrophe was paralleled by an ongoing financial collapse, described by the World Bank as one of the most severe global economic crises, registering the highest inflation rates encountered in the last 100 years. This collapse affected almost all small and medium enterprises - mine included. Of course, the economic crisis was further compounded because of COVID-19 which crippled Lebanon and the whole world for two long years. Despite the craziness and hardship, I continued to pursue my Ph.D., now dearly needed as a survival tool, at a time when everything around me seemed to be falling to pieces.

It is amazing how the human brain functions under pressure! No, it does not surrender. But it also does not function with full capacity as it cannot isolate itself from what is happening around it; it rather oscillates in a numbing in-between. I would say that this was my status while working on my Ph. D – a rollercoaster. ups and downs, both physically and emotionally. I would be full of enthusiasm and creativity at one moment and during the next, I would be playing a mind-numbing free arcade game to escape reality. Those six years, during which I was working on my Ph.D. taught me that this long and tedious work is done *only* one step at a time. It resembles building the renowned wall of China – one bolder at a time- and in my case while riding that bloody roller coaster. Another realization is that no matter, how much effort you put in, or the time you spend on your manuscript, it is all in vain until you place that last bolder to finish it all.

Through this long endeavor, I was accompanied and aided by an "unofficial" team of family members, friends, colleagues, and even total strangers. My main support came from my significant half, Dolly, that God-sent person into my life. Dolly assumed different roles at different times throughout my Ph.D., shifting from a partner-in-crime to a shrewd advisor, a venting recipient, a colleague advising on time management, of course, my conscience at times when I was wasting hours doing nothing, and my guardian angel putting me back on track with her famous “Yalla, you're almost finished”. Yet, most importantly she surrounded me with her unconditional love and understanding at all moments and all times- THANK YOU, LOVE.

Marc and Luca, my two boys, were my biggest motivation. As a team, Dolly and I will always try to do what is best for them. Any ray of hope we glimpse and deem good for their benefit we try to grasp- This Ph.D. journey fits perfectly in this philosophy.

My parents and in-laws were also avid supporters. My father, though suspicious of what I was doing in the greenhouse -ex-situ site was always supportive and catered to the needed technical requirements. My mom, on the other hand, was always ready with comfort food and beverages. My in-laws pushed me onwards with regular inquiries, warm wishes, and prayers. THANK YOU.

As for the academic support, I say, without hesitation that I would have never progressed an inch without the support, guidance, and encouragement of my advisors.

Dr. Carla Khater helped me through, advising, guiding, and most importantly, offering contacts and opening doors. My acquaintance with Carla spans far back in the time of almost two decades. I still remember that lively spring day when I met her with her brother at the Red Cross, where we both were proud young volunteers. Even back then, I was captivated by that beautiful smile and wild-spirited nature, maturing with time into a respected scientist and a proud mom. Dr. Khater's positive attitude and solution-oriented approach were much needed throughout the Ph.D. process and have helped give me the necessary push in times of doubt. THANK YOU.

Dr. Khater introduced me to Dr. Dutoit. The first encounter with Thierry was in a hotel lobby here in Beirut. That meeting is still vivid in my memory, especially at the moment when I saw an imposing figure stepping out of the elevator, embracing a broad smile. From that instant, I knew we were destined to have a harmonious academic relationship. Thierry was that perfect and much-needed balance in this long endeavor of mine. His vast academic experience, paralleled with an extensive practical field background, enabled us to manipulate our experiment – especially after my several initial failures –materializing it into solid concrete science work. If one day I am asked about what I treasure most of those memories with Thierry, I would answer without hesitation- *his remarkable understanding of situations, humane character, and kindness*. Thierry is a person that I am honored to have known, deeply cherish, and will grab as a lifelong friend/ mentor. He was always capable of perfectly balancing those two aspects of our

association academic and friendship, being a harsh academic tutor when needed and a kind considerate friend on a personal level. He never mixed those two aspects, never bargaining on the quality of academic deliverables, but always with that maturity and ability to evaluate things based on circumstances rather than rigidity. I met Thierry as an advisor and was honored to hold him as a dear member of our family. THANK YOU, MY MENTOR & BROTHER.

Another supporting pillar was Dr. Elise Buisson. Elise's capability to think big while operating numbers and figures is almost legendary. Her assistance with the statistical analyses made *all* the difference— especially for a dinosaur in the subject like me. The hurdles that I faced towards the end of the experiment were smooth by the one and only Dr. Buisson. THANK YOU

I am also thankful to Dr. Tania De Almeida, whose contribution enabled the transformation of those nightmarish statistical figures into neat, simple, and elegant graphs and tables. This was a blessing, to say the least. THANK YOU.

As for friends' assistance, a few precious people were next to me on my journey.

Mr. Jimmy. Joujou. *Ya Mr. Joujou, with all honesty, I can attest that I would have never pulled this quest without you.*

I still remember calling Jimmy at the plant collection phase, in my first ex-situ experiment, asking for his help, assuring him that this was “max a 2- 3 hours job, accomplished in a one-afternoon session.”. Enthusiastically Jimmy came to help and ended up helping me for the next 22 days.

Jimmy was ever-present, positive, and supportive, and always escorted by a whole bundle of practical solutions for any problem we *might* face, living up to his infamous quote “An engineer always comes fully equipped.”- THANK YOU

The gallant deeds of Jimmy were complemented by those of his significant half, Nelly- aka the Excel wizard. Speed, broad grasp of matters, and calmness were the magic formula that helped sort the collected filed data into readable tables, ready to be analyzed. THANK YOU

Miss Sophie Mansour, allocated innumerable hours aiding me, time and again, proofreading, tabling, and formatting my never-ending articles. Sophie has been a never-tiring spirit, meticulous and a knowledgeable scientific writer *whose -positive attitude I could always count on.* THANK YOU

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The assistance of all those aforementioned fantastic people allowed me to reach the end of this quest – the fruits of which I place in your hands – My final Ph. D manuscript.

As a great philosopher once said, “Hold this manuscript well, read with your brain, admire with your sentiments, spread the small knowledge it added, but retain its mischiefs to yourself.”

And I shall retain those mischiefs to myself!

Houssam Shaiban

TABLE OF CONTENTS

Foreword.....	I
Acknowledgment	III
List of Figures	1
List of Tables	6
GENERAL INTRODUCTION.....	7
Problem Statement.....	9
General hypothesis and chapters outline	9
Thesis outline	13
Literature Review.....	15
Restoration ecology, hopes, and limits.....	15
‘Nurse Plants’ concept as a restoration tool.....	16
Semiarid Mediterranean environment habitats.....	34
Lebanon, a multi-challenging environment.....	37
METHODOLOGICAL APPROACH	45
Why in an ex-situ mesocosm setting, and what are its limitations?	46
The competition index used, means of calculation, and its limitations	46
CHAPTER ONE	52
Hydroseeding for Restoring Degraded Semi-Arid Mediterranean Environments: A Review of Challenges	52
Abstract.....	54
Keywords: Abiotic factors, biotic factors, limitations, success, failures, restoration techniques.	54
Introduction	55
Methods.....	58
Results.....	58
Hydroseeding techniques and their limitations.....	58
Abiotic factors affecting hydroseeding.....	59
Biotic factors affecting hydroseeding	66
Discussion.....	71
Supplementary material	72
TRANSITION TO SECOND PAPER	83
CHAPTER TWO	82
Is <i>Trifolium subterraneum</i> L. a potential nurse plant for restoring soil and degraded Mediterranean grasslands on former quarries in Lebanon?.....	83

Abstract.....	85
Aim	85
Method	85
Important Findings.....	86
Conclusion.....	86
Keywords: <i>Trifolium subterraneum</i> , nurse plant, facilitation, competition, soil properties, target plant	86
Introduction	87
Materials and Methods.....	88
Study site.....	88
Potential nurse plant.....	89
Target species for restoration.....	91
Experimental design.....	94
Soil and seed collection.....	94
Mesocosm experimental site.....	98
Design and procedure.....	98
Soil preparation and analyses.....	99
Performed experiments.....	100
Plant measurements	104
Statistical analyses	105
Soil statistical analyses.....	105
Plant statistical analyses	105
Results.....	106
Soil results.....	106
RII results.....	113
Discussion.....	116
Soil results.....	116
RII results.....	118
Conclusion and perspectives	120
Illustrations - Tables.....	122
Illustrations	122
Tables.....	123
Intermediate section.....	128
Plant species used in the experiments described in Chapters 2 & 3.....	128

TRANSITION TO THIRD PAPER.....	132
CHAPTER THREE	134
Assessing the effect of neighbors on two potential nurse plants taking soil and priority effects into account.....	132
Abstract.....	136
Aim	136
Method	136
Important Findings.....	137
Conclusion.....	137
Keywords: <i>Trifolium subterraneum</i> , <i>Melica inaequiglumis</i> , nurse plant, facilitation, competition, soil properties, target plants.	137
Introduction	138
Materials and Methods.....	142
Nurse plant species used	143
Neighbor species.....	144
Experimental design.....	147
Plant measurements	152
Analyses	153
Protocol used	153
Statistical analyses	153
Results.....	154
Effect of neighbor plants on <i>Trifolium subterraneum</i> biomass (RII_{response})	154
Effect of neighbor plants on <i>Melica inaequiglumis</i> biomass (RII_{response}).	155
Discussion.....	156
Effect of neighbor plants on <i>Trifolium subterraneum</i> biomass	156
Effect of neighbor plants on <i>Melica inaequiglumis</i> biomass	158
Conclusion and perspectives	158
Potentials of using <i>Trifolium subterraneum</i> as a nurse plant.	158
Potentials of using <i>Melica inaequiglumis</i> as a nurse plant.	159
Tables – Illustrations	161
Tables	161
Illustrations	163
Discussion, conclusion, and perspectives	165
Contribution towards a better understanding of quarrying status in Lebanon	166
Contribution of the thesis to practical ecological restoration practices	167

Challenges facing hydroseeding practice in restoring semiarid Mediterranean environments.....	167
Native species as potential 'Nurse Plants' used in restoring degraded quarries	167
Research perspectives	170
Repetition of the same experiments in an in-situ setting- the quarry	171
Implementing the results of the ex-situ experiments in an in-situ setting.....	172
Effect of inoculation of <i>Trifolium subterraneum</i> seeds with <i>Rhizobium</i> sp.....	172
Testing the priority effect principal	173
Bibliography	174

LIST OF FIGURES

Figure I. 1. Schematic representation of the general organization of the thesis.....12

Figure I. 2. Overview of the organization of the different sections and chapters presented in the manuscript. 14

Figure L. 1. Conceptual model of occurrence of positive interactions in natural communities (Bertness & Callaway, 1994).....20

Figure L. 2. A theoretical framework for the biotic and abiotic mechanisms of nurse plant effects through their life (from Filazzola and Lortie, 2014)..... 33

Figure L. 3. Biodiversity hotspots in the Mediterranean Basin (From Medail & Quézel, 1999).... 36

Figure L. 4. Location of the study area- Beqaa Plain in Lebanon 40

Figure L. 5. The intact side of the quarry, consisting of natural cliffs and former old cultivated terraces not damaged by quarrying and embracing an array of native overgrazed vegetation. (Shaiban, IMBE)..... 41

Figure L. 6. Another angle of the intact side of the quarry, consisting of natural cliffs and former old cultivated terraces not damaged by quarrying and embracing an array of native overgrazed vegetation. (Shaiban, IMBE). 41

Figure L. 7. The quarry side consists consisting of severely degraded areas due to quarrying. (Shaiban, IMBE)..... 42

Figure L. 8. Another angle of the side of the quarry shows the impact on soils and vegetation. (Shaiban, IMBE)..... 42

Figure L. 9. Geologic map of the abandoned quarry locality in Maqneh and the surrounding (Maqneh Report- CNRS)..... 43

Figure M. 1. Location of chapter one in the general organization of the thesis.....49

Figure 1. 1. Utilizing the hydroseeding technique as a restoration tool on a steep road cut slope (Martin et al., 2002). 56

Figure 1. 2. The Mediterranean Basin with its 22 bordering countries 56

Figure M. 2. Location of chapter two in the general organization of the thesis.....82

Figure 2. 1. <i>Trifolium subterraneum</i> plant tested as a potential nurse plant. (Shaiban, IMBE)	89
Figure 2. 2. The various target species used in the study, all are abundant in the Mediterranean grasslands.....	92
Figure 2. 3. General location of the quarry site where the soil was extracted- Maqneh, Beqaa Plain, Lebanon. (Modified from Ecomed, 2016).....	95
Figure 2. 4. Quarry, the degraded ecosystem. (Shaiban, IMBE)	96
Figure 2. 5. Reference overgrazed old grassland ecosystem in formerly cultivated terraces located next to the quarry. (Shaiban, IMBE)	96
Figure 2. 6. Transporting collected soil from the quarry and nearby reference ecosystem to the experimental site. (Shaiban, IMBE).	97
Figure 2. 7. The general setting of the site location of the experiment, along with the tunnel greenhouse. Zahrieh village, Mount-Lebanon, Lebanon (Shaiban, IMBE).....	98
Figure 2. 8. Seed germination in trays. (Shaiban, IMBE).....	101
Figure 2. 9. Schematic representation of the procedure for the 3 years experiment.....	102
Figure 2. 10. Dry Biomass contents measured in-situ degraded soils and reference soils at set-up, with the different treatments applied in the pots to the degraded soil at the time of set-up, without soil improvement and later with soil improvement (F=20.5, P<0.001). TS is <i>Trifolium subterraneum</i> - TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.....	107
Figure 2. 11. Total Nitrogen contents measured in-situ degraded soil at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement (F= 52.5, P<0.001). TS is <i>Trifolium subterraneum</i> - TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.....	108
Figure 2. 12. Soil Carbon analyses performed for in-situ degraded soil and reference soil at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement (F= 20.5, P<0.001). TS is <i>Trifolium subterraneum</i> - TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.....	109
Figure 2. 13. Available Phosphorus contents measured in-situ degraded soil and reference soil	

at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement (F= 83.9, P<0.001). TS is *Trifolium subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.....110

Figure 2. 14. Potassium contents measured in-situ degraded soil and reference soil at the time of set-up, and the different treatments applied in the pots to the degraded soil without soil improvement and later after soil improvement (F= 28.3, P<0.001). TS is *Trifolium subterraneum*- TR is Target plants. - “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.....111

Figure 2. 15. Effect of *Trifolium subterraneum* as a nurse plant, and soil improvement on target *T. subterraneum* biomass grown on degraded soils ($X^2=0.30$, $p<0.001$, $n = 5$). Bars sharing a letter were not significantly different from each other ($p<0.05$). “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement. Without *T. subterraneum* = Without *T. subterraneum* as a nurse plant; With *T. subterraneum* = With *T. subterraneum* as a nurse plant.....113

Figure 2. 16. Effect of *Trifolium subterraneum* on neighbor species biomass depending on neighbor species identity on year 1 (F=2.89, $p=0.034^*$): mean RII effect per replicate pot ($n = 5$). The horizontal line marks RII = 0, above which positive RII values indicate facilitation and below which negative values indicate competition. Species sharing a letter were not significantly different from each other ($p<0.05$). Box-plots colored light blue show RII significantly different from 0 (tested by Wilcoxon test). 114

Figure 2. 17. Effect of *Trifolium subterraneum* on target species biomass depending on target species identity after soil improvement (F=12.65, $p<0.001^{***}$). mean RII effect per replicate pot ($n = 5$). The horizontal line marks RII = 0, above which positive RII values indicate facilitation and below which negative values indicate competition. Species sharing a letter were not significantly different from each other ($p<0.05$). Box-plots colored light blue show RII significantly different from 0 (tested by Wilcoxon test). 115

Figure 2. 18. Effect of *Trifolium subterraneum* on target species biomass depending on soil type after soil improvement (F=8.30, $p=0.006^{**}$). Mean RII effect per replicate pot ($n = 5$). The horizontal line marks RII = 0, above which positive RII values indicate facilitation and below which

negative values indicate competition. Soil types sharing a different letter were significantly different from each other ($p < 0.05$). Box-plots colored light blue show RII significantly different from 0 (tested by Wilcoxon test). 116

Illustration 2. 1. Experimental design, plant arrangements in pots.....122

Figure M. 3. Location of chapter three in the general organization of the thesis.....131

Figure 3. 1. Potential nurse plants used in the experiment.....142

Figure 3. 2. Neighbor plants used in the experiment.....144

Figure 3. 3. The two sites where seeds and soil were collected.....146

Figure 3. 4. The general setup of the mesocosm experiment in a tunnel- greenhouse. (Shaiban, IMBE).....147

Figure 3. 5. Extraction, transportation, and preparation of soil from reference and degraded sites. (Shaiban, IMBE).....148

Figure 3. 6. Soil preparation, filling, and irrigation installation. (Shaiban, IMBE).....148

Figure 3. 7. Seedling germinating, hardening, and planting. (Shaiban, IMBE).....149

Figure 3. 8. Response of *Trifolium subterraneum* biomass to neighbors affected by the type of soil and planting date ($F=9.03$, $p=0.005^{**}$) ($n=4$). The horizontal line marks $RII=0$, above which positive RII value indicates facilitation and below which negative values indicate competition. Bars sharing a letter were not significantly different from each other ($p < 0.05$). Boxplots colored in blue show RII significantly different from 0 (tested by Wilcoxon test).....153

Figure 3. 9. Response of *Melica inaequiglumis* biomass to neighbors affected by the type of soil and planting date ($F=7.04$, $p=0.014^{*}$) ($n=4$). The horizontal line marks $RII=0$, above which positive RII value indicates facilitation and below which negative values indicate competition. Bars sharing a letter were not significantly different from each other ($p < 0.05$). Boxplots colored in blue show RII significantly different from 0 (tested by Wilcoxon test).....154

Illustration 3. 1. Plant arrangements in pots.....**Error! Bookmark not defined.**

Illustration 3. 2. Schematic design for the experiment. Where *T. sub* is *Trifolium subterraneum*- *M. ina* is *Melica inaequiglumis*- NC is Neighboring Community with 1, 3, or 4 plants of different species/ pot.....162

LIST OF TABLES

Table 1. 1. Primary and secondary keywords used to filter and select the papers used in the methodology.....	72
Table 1. 2. Main factors extracted from the literature review that might be affecting the success or failure of the hydroseeding procedure in a semiarid Mediterranean environment.	79
Table 1. 3. Factors affecting hydroseeding results in a semiarid Mediterranean environment (NA - Natural Abiotic factors affecting hydroseeding; HA - Human-induced Abiotic factors affecting hydroseeding; HB - Human-induced Biotic factors affecting hydroseeding)	79
Table 2. 1. Seed germination percentages based on coleoptile emergence as a proxy of germination under controlled laboratory conditions during an 8 weeks period.....	123
Table 2. 2. Results of physical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up, and with the different treatments applied in the pots to the degraded soil without soil improvement. TS is <i>Trifolium subterraneum</i>	123
Table 2. 3. Results of chemical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up, with the different treatments applied in the pots to the degraded soil without soil improvement, and after soil improvement. TS is <i>Trifolium subterraneum</i> - TR is Target plants.....	124
Table 3. 1. Results of physical soil analyses performed for in-situ degraded soils and in-situ reference soils in 2018.....	159
Table 3. 2. Results of chemical soil analyses performed for in-situ degraded soils and in-situ reference soils in 2018.....	159
Table 3. 3. Seed germination percentages based on coleoptile emergence as a proxy of germination under controlled laboratory conditions during an 8 weeks period.....	160

GENERAL INTRODUCTION

Problem Statement

The Mediterranean Basin (MB), with numerous, faulted and folded limestone, along with calcareous formations has created in diverse locations a variety of habitats ranging from sea level to alpine habitats, accumulating around 25,000 plant species (Vogiatzakis et al., 2006), half of which are endemic (Quézel, 1985). Modern human colonization of the basin 10,000 years ago was crucial in both cultural and environmental history. The domestication of plants (such as barley and wheat) along with animals (goats, sheep, and cattle) led to a permanent modification in the ecosystem (Mannion, 1999). This pressure has not relented since.

Located at the eastern end of the MB, Lebanon, with around 2600 plant species (of which 12% are endemic (MoE/UNDP/ECODIT, 2011), scattered at varied topographies, altitudes, and diverse ecosystems (MoE/ECODIT, 2002)), is considered a biodiversity hotspot (Myers et al., 2000). However, this ecosystem was exploited by humans for millennia leading to habitat loss, fragmentation, quarrying, deforestation, pollution, wars, refugee inflow (Ammar et al., 2016), random urbanization, and climate changes (Faour, 2015; MoE/UNEP/GEF, 2016).

Of all previously cited ecological concerns, quarries are considered one of those extreme and pressing environmental issues facing Lebanon. Approximately 1,300 quarries are scattered throughout the country, disturbing the landscape patterns and destroying natural habitats (Khater et al., 2003; Khater, 2004). Unfortunately, few quarries have been restored or rehabilitated, and few researchers are working on rehabilitation and/ or restoration (khater, 2004).

General hypothesis and chapters outline

The primary objective of the thesis is to evaluate, through a literature review, the limits of one current practice, hydroseeding, as a restoration tool utilized in a semiarid Mediterranean environment. Accordingly, the second objective is to assess the possibility of replacing costly and sometimes inappropriate techniques, such as hydroseeding in semiarid Mediterranean environments with practical nature-based solutions. Ultimately, as Dutoit (2014) suggested, to restore "nature by nature" i.e. using natural ecological engineers such as nurse plant species.

This thesis is structured around three chapters (Figure I. 1.). The first chapter is an extensive literature review of both pros and cons of adopting the hydroseeding technique as a restoration tool in semiarid Mediterranean environments. The second chapter focused on the potential role of a legume native to Lebanon, *Trifolium subterraneum* L., as a nurse plant to assist the growth of various native neighbor plants for restoring degraded areas, such as abandoned quarries. Finally, the third chapter of the thesis assessed the effect of neighbor plants on two nurse plants, *T. subterraneum*, and *Melica inaequiglumis* Boiss., in diverse soil types, varied complexities, and different planting dates.

Therefore, the three main questions and their subsequent analysis each comprised a chapter:

- 1. Is the Hydroseeding technique suitable for restoring degraded semiarid Mediterranean environments? What are the challenges facing its utilization? And what are some recommendations for its application in such harsh environments?**

A literature review assessed whether hydroseeding, a current restoration technique, is suitable in semiarid Mediterranean Environments (chapter 1). This review spanned the last three decades (1990-2020), covering approximately 100 of the most relevant published papers. From this analysis, several legitimate inquiries surfaced, such as the most important variables affecting hydroseeding in a semiarid Mediterranean environment Are those factors biotic or abiotic? Natural or human-influenced? Could any recommendations be proposed to improve the technique?

- 2. For restoration purposes, can *T. subterraneum* (a legume native to Lebanon) play the role of a nurse plant assisting in establishing different target neighbor plants intended to restore degraded environments?**

After reviewing hydroseeding as a technique used in semiarid Mediterranean ecosystems, a natural restoration technique was investigated– the nurse plant. The assessment, undertaken in an ex-situ setting, analyzed the contribution of a potential nurse plant, *T. subterraneum*, to soil properties and neighbor plants established in soil collected from a quarry, as a degraded ecosystem, and a nearby grassland, as a reference ecosystem (chapter 2), with the following

subsequent questions formulated: (1) Can it improve properties of degraded soil compared to reference soil ?; (2) Being an annual, accordingly, after growing and dying out, with dried matter incorporated into the soil, can it further improve soil physical and chemical properties ?; (3) Can it benefit neighbor plants present in its vicinity by improving various indicative traits, most important of which is the biomass?

3. Approaching further toward a natural plant community setting with the interaction of two nurse plants (separately) with neighbor plants, a new set of questions materialized: (1) What is the effect of the neighbor plants on the two different nurse plants? (2) At three varied community complexity levels? (3) In two different soil types? (4) when altering planting dates between nurse and neighbor plants?

Having tested the potential nurse plant *T. subterraneum* in assisting the growth of nearby neighbor plants of four individuals of the same species (chapter 2), the next logical step forward would be a “more realistic imitation” of natural plant communities. This notion was performed by assessing two plants (a vetch, *T. subterraneum*, and grass, *M. inaequiglumis*) as potential nurse plants (chapter 3), questioning the effect of other native plants at different densities (low, medium, and high plant concentrations) on them, in two varied soil types, a reference, and a degraded one, and at different planting intervals, to determinate the existence of any potential priority effects.



Figure I. 1. Schematic representation of the general organization of the thesis.

Thesis outline

The whole thesis is divided into four sections (Figure I. 2.):

Section 1 will comprise a general introduction, including a problem statement and an extensive literature review encompassing the various research concerning the theory of facilitation vs. competition in plant communities. The debatable notion of the facilitation effect with respect to the stress gradient hypothesis was highlighted. Also, the types of facilitation mechanisms, whether of direct or indirect type, are reviewed. The nurse plant concept, as a theory, will be examined with examples. Furthermore, the semiarid Mediterranean habitats, with thousands of years of human impact, are explained by emphasizing challenges and highlighting hopes via ecological restoration practices. The section concludes with the multi-challenges facing the environment in Lebanon and highlights the present status of its quarries.

In **Section 2**, methodological approaches used in the experiment were investigated, highlighting why the experiments were performed in ex-situ setting and explaining how measurements were taken.

Section 3 is a succession of three chapters (1, 2, and 3). **Chapter 1** assesses hydroseeding as a restoration tool in the semiarid Mediterranean environment. **Chapter 2** evaluates the use of the native legume, *T. subterraneum*, as a potential nurse plant for other native plant species found in the grasslands of Lebanon. **Chapter 3** assesses the effect of neighbor plants on two native plants used as potential nurse plants, investigating their influence at different densities and soil types while taking the priority effect concept into account.

Section 4 concludes the thesis and highlights fundamental and practical perspectives, suggesting further possible research steps and ending with a general bibliography.

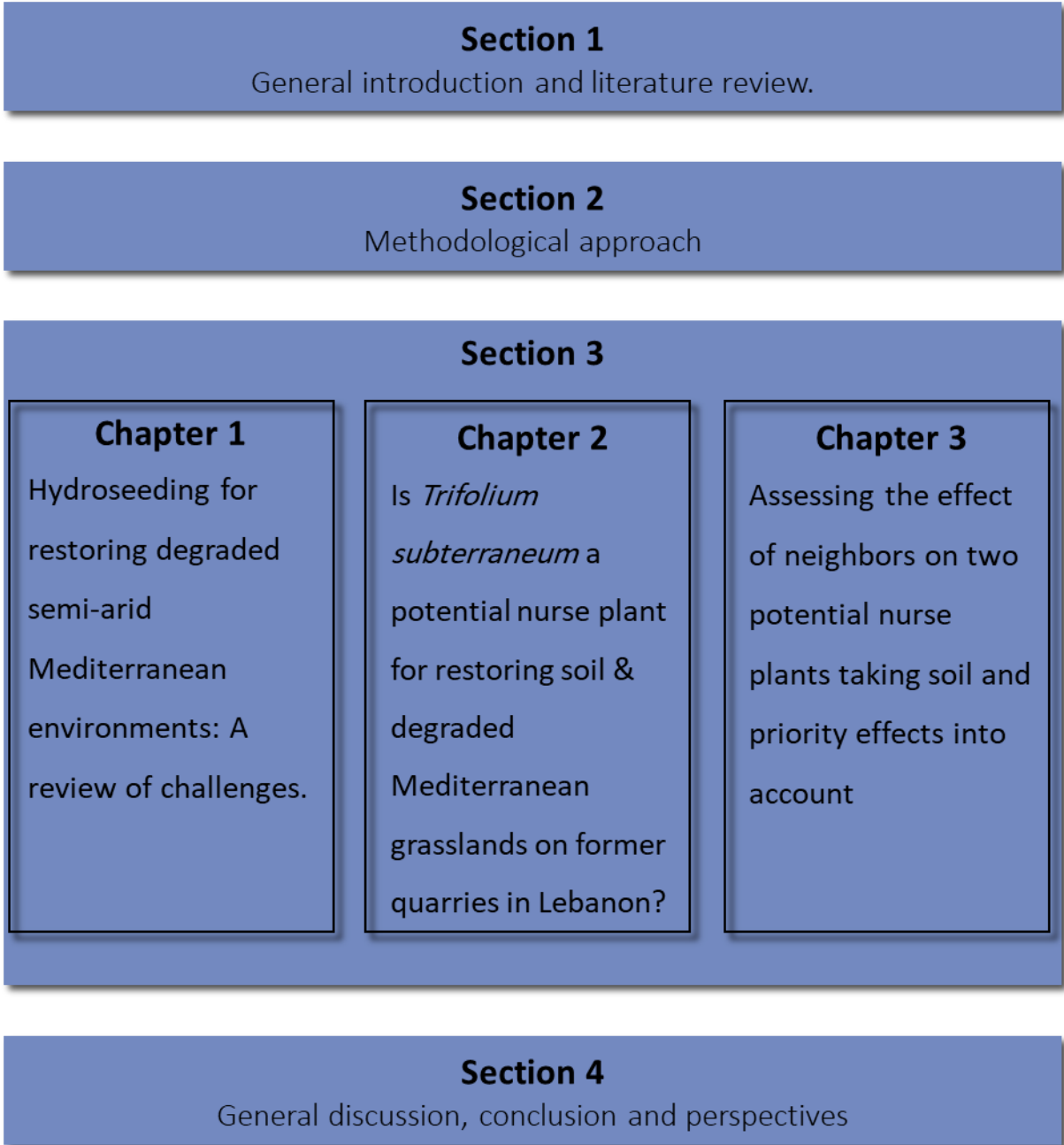


Figure I. 2. Overview of the organization of the different sections and chapters presented in the manuscript.

Literature Review

Restoration ecology, hopes, and limits

Even back in 2010, almost two-thirds of the globe's ecosystems were already considered degraded, due to failures in investing and reinvesting in their productivity, health, and sustainability (Dutoit, 2010). In a meta-analysis study, Benayas et al. (2009) evaluated, in a broad range of ecosystems throughout the globe, the effectiveness of different restoration actions of 89 restoration projects undertaken to enhance both biodiversity and ecosystem services. Results revealed that ecological restoration increased the provision of biodiversity and ecosystem services by 44% and 25%, respectively. Unfortunately, several unsuccessful restoration projects are due to failure in recognizing and addressing uncertainties, paralleled by inappropriate time scales, wherefore, ecological restoration tries to achieve in a few years what may need decades or even hundreds of years under natural circumstances (Hilderbrand et al., 2005, Walker et al., 2007). Consequently, ecological restoration should not focus on restoring to some initial state but instead support a more flexible approach of accepting a dynamic ecosystem concept, ultimately focusing on repairing degraded systems to a potential extent. Hilderbrand et al. (2005) highlighted five common restoration myths to avoid: (1) Carbon copying (the assumption that community assembly is predictable with the existence of a single endpoint). (2) The field of dreams (the notion of solely focusing on physicochemical conditions, and hereafter the systems will self-organize). (3) Fast forward (considering that succession and ecosystem development can be fast-tracked). (4) Cookbook (where overused methodologies are not sufficiently validated). (5) Command and control myth (the false belief that nature is controllable). Therefore, as Hobbs & Harris (2001) neatly stated, restoration ecology, to be successfully practiced as part of humanity's response to continuous ecosystem changes and degradation, needs to scale to the challenges of coordinating science, practice, and policy.

One significant notion that could be of practical use in restoration ecology (and is tested in this manuscript) is the "priority effect" concept, defined as the effect created by the arrival order of different species to a specific site. The arrival order can have a paramount role in the assembly of a community due to the effect of those early arrivals on the performance of later ones (Hess et al.,

2019). Since the outcome of the “priority effects” could be different based on the identity of the earlier and later arriving species (Dickson et al., 2012; von Gillhaussen et al., 2014; Stuble & Souza, 2016), consequently, in several cases, failure to account for the “priority effect” concept might lead to restoration failures (Young et al., 2001; Temperton et al., 2004; Wilsey et al., 2015). Taking such effects into account in restoration projects might be a way to improve restoration success, especially when using native species as nurse plants for their abilities to facilitate or increase the installation and the growth of other species (Hess et al., 2019).

‘Nurse Plants’ concept as a restoration tool

Facilitation- a key phase in plant dynamics in harsh environments

The precept that plants needed to be released from the struggle of competition was the fruit of a more than 100-year-old debate between Frederic Clements and his contemporary Henry Gleason, both being ecologists from the early 1900s. What they both endeavored to describe, in different ways, were the constituents of a plant community and what determines how plants in a community grow together and why (Benyus, 2017, as cited in Hawken, 2017). Plant-to-plant interactions concept was introduced initially in the early twentieth century by Pearson (1914) after observing better post-fire regeneration of the conifer *Pseudotsuga menziesii* among clones of *Populus tremuloides* due to the amelioration, by the latter, of various abiotic conditions such as shade, wind speed, and evaporation rates. This concept was, and still is, a major disagreement issue between advocates of the “holistic ecology” of Frederic Clements and the “reductionist” or “individualistic ecology” of Henry Gleason. Clements saw plants as intertwined communities with facilitation flowing among them, such as the nursing of tiny seedlings under a tree by protecting them from the harsh sun and wind, also enriching the soil with fallen foliage- a notion he anointed “organismic” (Clements, 1916). Whereas Gleason, contrary to what preceded, coined what is known as the “individualistic concept of ecology” theory. He saw Clements communities as merely simple coincidence or random bodies dispersed and arranged according to their soil, water, and light needs. Gleason saw no mutual aid but instead competition dominating among plants (Gleason, 1917, 1926, 1939), stating that a plant community is scarcely even a vegetational unit, merely a coincidence (Gleason, 1926), adding, “it

seems that the vegetation of a region is not capable of complete segregation into definite communities, but that there is a considerable development of vegetational mixtures”.

Throughout most of the history of ecology, individualism and competition among plants were considered the principal interactions shaping plant communities. This belief is apparent since plants essentially utilize the same vital but limited resources that get scarcer upon consumption. Hence, the competition must be an intense and prevalent interaction among plants (Scott, 2009). Unfortunately, for years the facilitation concept between plants was neglected and dropped from mainstream ecology in favor of the endorsement of both the individualistic (Gleason, 1926; Whittaker, 1956) and the competition theory (Grime, 1974; Tilman, 1982). Almost throughout the twentieth century, competition, by far, was the most studied biotic interaction, especially by plant community ecologists- a bias reflected by a towering figure of up to 90% of the published papers focusing on the subject (Michalet & Pugnaire, 2016). As Bertness & Callaway (1994) so neatly stated, “Fascination with competition has focused attention on communities where competition is conspicuous”. Favorably, from the mid-nineties of that same century, things slowly started to shift. In a landmark study, Simard et al. (1997) used reciprocal isotope labeling to verify a bidirectional allocation between the ectomycorrhizal tree species *Betula papyrifera* and *Pseudotsuga menziesii*. In an in-situ setting, Simard exposed the seedlings *P. menziesii* to Carbon-14 and *B. papyrifera* to Carbon-13. The results showed that both radioactive Carbons were absorbed by the seedlings, transformed into sugars, and later exchanged between the different seedlings (verified by a Geiger counter). Carbon-13 from the *B. papyrifera* traveled to the *P. menziesii*, while Carbon-14 traveled from the *P. menziesii* to the *B. papyrifera*. This pioneering work proved that plants of different species collaborate - via a vast underground fungal network- by exchanging different minerals such as carbon, nitrogen, phosphorus, water, and even defense compounds (Benyus, 2017, as cited in Hawken, 2017). Adding to what preceded, more and more evidence confirmed that facilitation – alongside competition – also had a major role in shaping plant relationships amongst each other and in communities (Bertness, 1988, 1991; Bertness & Shumway, 1993; Bertness & Hacker, 1994). Callaway et al. (1991) investigated whether randomly scattered oaks in Californian rangelands should be felled, to eliminate competition with pasture grasses. Meticulous measurements of various factors such as light, temperature, soil nutrients, soil moisture, and fine roots distributions revealed that

productivity is twenty to sixty times greater under the oaks than in open grasslands due to facilitation via litterfall and throughfall, rendering the term facilitation as a process rather than a purpose (Callaway, 2007). In the two decades to follow, the preceded publications, as well as a key paper by Bertness & Callaway (1994), ignited further interest in the subject of facilitation, reflected by an increase in the average number of studies/ years about facilitation in the plant community from barely 1% in 1981 up to 24% in 2015 (Michalet & Pugnaire, 2016). Researchers started raising additional inquiries about evidence of facilitation and its interactional processes in plant communities, mechanisms of facilitation, and the consequences of facilitation for plant communities. (Callaway et al., 2005). The facilitation concept, proposed by Clements (1916) and later by Connell & Slatyer (1977), was in the context of facilitation of one successional stage by the preceding stage. In other words, such facilitation occurs only during primary successions when early colonizers improve harsh physical conditions (Brooker et al., 2008). However, once earlier colonists are established, would they halt the incorporation of new individuals by inhibition according to a model of succession? (Connell & Slatyer, 1977). With time, especially during the last decade of the twentieth century, a developing body of research highlighted the importance of facilitative interactions not only during successional changes but also as important plant regulators in their environment and community arrangement in stable environments (Bertness & Callaway, 1994; Callaway, 1995, 1997; Brooker & Callaghan, 1998). Building on what preceded, hypotheses that if the presence of a species is critical for the existence and performance of another species, then the community shaped through these interactions does not fit the classical definition of an “individualistic” entity (Choler et al., 2001). Such legitimate arguments led to the rise of an important question: If assemblies of organisms display interdependence, then how interdependent are they? (Callaway, 1997).

Stress Gradient Hypothesis (SGH)

This renewed interest in plant-plant facilitation produced more proof that such facilitation not only ameliorated the local environment into a more favorable one (Stachowicz, 2001) but also exposed an even more critical concept-*Facilitation escalates with increased environmental stresses* (Figure L. 1.). south-facing vs. west-facing slopes in rocky plant communities (Callaway et al., 1996), dry vs. adjacent mesic sites (Holmgren et al., 2000), higher vs. lower depths of coastal ecosystems (Bertness et al., 1999), or high vs. low altitudes in alpine and semiarid environments (Pugnaire & Luque, 2001;

Callaway et al., 2002), also salt marshes, deserts, and arctic or alpine tundra habitats (Levitt, 1980), all have the severe and stressful environmental conditions as a shared feature affecting plants (Bertness 1988, 1991; Bertness & Shumway, 1993; Bertness & Hacker, 1994).

But what are stressful conditions for plants, and how are they defined? Stressful conditions are defined broadly as any external force rendering an individual or population less fit (Wiens, 1976), restricting the ability of producers to convert energy to biomass (Grime, 1977). It can be of a physiological nature, such as temperature, salinity, or drought conditions, or of a physical nature, like direct effects of wind, waves, and currents, or can be of biotic nature, such as competition, predation, and disease (Stachowicz, 2001). In situations, plants can alter various stressful conditions like micro-environmental surroundings, surface wind, fluvial flow, or improve soil fertility through organic matter, consequently enabling natural restoration of the abiotic environment (Davy, 2002; Whisenant, 2002). Alteration of a specific environment through the facilitation of already existing and established vegetation will effectively assist in the succession of new individuals into a community (Connell & Slatyer, 1977), affecting both abiotic and biotic environments (Callaway, 2007), directly or indirectly, ultimately, affecting the development or reproduction of one or more organisms positively (Bertness & Leonard, 1997). The fact that plant facilitation is not restricted to specific communities or biomes (Callaway, 1995), but is rather widespread in the natural world especially in severe environments, intrigued Bertness & Callaway (1994) to raise several fundamental questions: “Do positive interactions affect recruitment? Do these positive species interactions influence species distributions? Do positive interactions affect succession? Are positive interactions predictable features of natural communities?”. Eventually, proposing a conceptual model in which competition shifts to facilitation with increasing environmental severity, a model they anointed the Stress Gradient Hypothesis (SGH). They specified that the basic idea of the SGH revolves around facilitation, stating that it “should be particularly common in communities developing under high physical stress, and in communities with high consumer pressure”, adding, “where the physical environment is relatively benign and consumer pressure is less severe, positive interactions should be rare; as a result, competitive interactions should be the dominant structuring forces”. The hypothesis suggests that net competitive effects are more significant, or at least more intense (Brooker et al., 2005), in relatively benign low-stress environments. Whereas on the other hand,

facilitative effects are more vital in relatively severe, high-stress environments (Figure L. 1.). Kikvidze et al. (2006) clarified this concept as follows: “Under relatively benign abiotic conditions that permit rapid resource acquisition, competition may be more important. However, if severe physical conditions restrict resource acquisition, amelioration of severe stress by a neighbor may be more likely to favor growth than competition with the same neighbor”. The ranges of harsh physical conditions that could be ameliorated by plants are low nutrient levels, heat/ desiccation, soil moisture, soil oxygen, osmotic stresses, and disturbances (Bertness & Callaway, 1994).

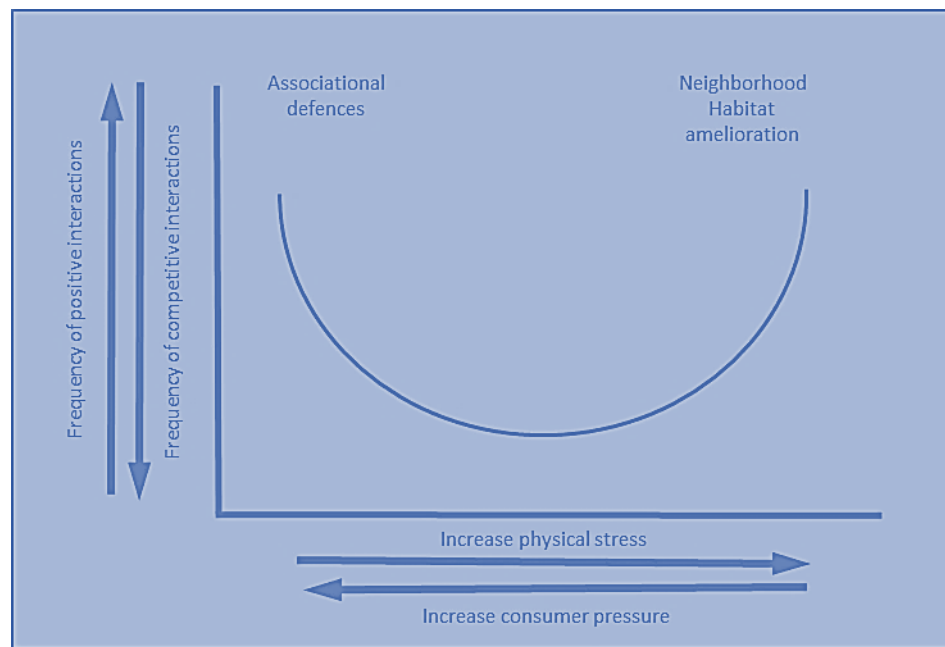


Figure L. 1. Conceptual model of occurrence of positive interactions in natural communities (Bertness & Callaway, 1994).

Several studies attempted to verify the SGH under varied conditions and habitats. Greenlee & Callaway (1996) assessed the presence of facilitation or competition on a single target species of the rare endemic mustard plant (*Lesquerella carinata* var. *languida*- Brassicaceae) by bunchgrasses on xeric rocky slopes in Montana, USA. Results revealed the presence of facilitation by the grasses in dry and hot years compared to relatively benign years. In southeast Spain, Pugnaire & Luque (2001) evaluated SGH along an environmental gradient in a semiarid situation by investigating changes in competition and facilitation among *Retama sphaerocarpa* shrubs with respect to understory plant species. Outcomes indicated an alteration in the net balance from positive in the water-stressed and in-fertile environment to more neutral, even negative interactions in the more fertile habitat. In the

Mediterranean semiarid grasslands, Maestre et al. (2003) assessed both spatial and temporal differences in the positive, negative, and net effects of the perennial grass *Stipa tenacissima* on the evergreen shrub *Pistacia lentiscus*. The net effects of the former on the latter were continuously facilitative, where an increase in the harshness of the environmental conditions amplified the degree of facilitation in both space and time. In a four-year experiment, Gómez-Aparicio et al. (2004) tested SGH variability in both space and time. Results revealed that facilitation among shrubs and tree seedlings was not patchy or limited to a few plant species grouping and environmental conditions. Instead, it is a widespread phenomenon, with double the rate of seedling survival and 76% growth of seedlings planted under shrubs than in open areas. Whereas previous studies focused on inter-seasonal variations, Kikvidze et al. (2006) studied the effect of SGH within a single growing season with environmental conditions changing from benign to harsh in semi-natural subalpine hay meadows in the central Caucasus Mountains. Results revealed that during the benign first half of the growing season target plants without neighbors amassed significantly more biomass than individuals with neighbors- hence showing competition. As the second half of the growing season approached, with more hostile conditions prevailing, there was a shift towards facilitation through expressively less biomass accumulation for individuals without neighbors. In a large-scale trial over three years on the perennial grasslands in New Zealand, Wardle et al. (1999) removed subsets of functional groups or species and examined the reactions of other species. Most responses indicated competition; however, in winter, one of the species, *Trifolium repens*, was strongly affected by *Lolium perenne* removal- signifying competition. Whereas, during the summer season, with dryer conditions prevailing, the *T. repens* was strongly inhibited due to the removal of *L. perenne*-signifying facilitation. While the previously mentioned papers highlighted facilitation in adult plant interactions under harsh environments, Lortie & Turkington (2002) tested the facilitative effects of *Erodium laciniatum*, as seeds and seedlings, on germination and later on the community of an annual plant seed bank in the Negev desert. Results suggested that both *Erodium* seeds and seedlings acted as facilitators for the plant community by increasing the density and biomass of germinated plants and that interactions between seeds and between plants and seeds could influence plant community structure. Other studies broadly assessed SGH and the organization of plant communities along elevational and topographical gradients. Choler et al. (2001) investigated in the southwestern Alps the determining roles of competition and facilitation in the organization of the alpine-plant

community along elevation and topographical grades. Their results indicated that at high elevations plant community patterns, abundance, and distribution, were enhanced by positive and negative interactions among neighbor plants. The SGH concept has also been experimented with among non-vascular plants and bryophyte communities. Recreating bryophyte communities with naturally co-occurring mosses and liverworts, Mulder et al. (2001) tested interactions between different species in a diverse range and productivity under constant conditions and droughts. Results indicated no association between species richness and biomass under constant conditions, but when communities were exposed to droughts biomass, the increased, and species richness was detectable. SGH was also assessed at large spatial scales for the ability of benefactors to provide stable microclimates i.e. the large-scale analyses of whole communities. In the Sonoran Desert, Mexico, Tewksbury & Lloyd (2001) studied how *Olneya tesota*, a long-lived desert tree, could structure plant communities by promoting biological diversity. Results revealed that under xeric conditions, *O. tesota* canopies had strong positive effects on both plant biodiversity and abundance, along with small but significant positive effects on the size of plants, therefore showing facilitation in extreme environments. Whereas in mesic environments, the *O. tesota* trees had negligible effects on perennial plants and a negative effect on ephemeral ones, signifying competition.

Critics of Stress Gradient Hypothesis

The concept of facilitation under stressful environmental conditions proposed initially by Bertness & Callaway (1994) was not criticism-free. In 2005, Maestre et al. (2005) published a meta-analysis review of all relevant studies published between 1970 and 2004, assessing the effects of stress on the outcome of plant-plant interactions in arid and semiarid environments. Their data revealed that effects were due to the supply of one of three primary resources, water, nutrients, and light, tested by creating four separate categories of response variables: survival, density, growth, and fecundity. Their results indicated that in none of the examined data, the magnitude of the net effect provided by neighbors (whether positive or negative), was higher under high abiotic stress conditions, therefore, concluding that facilitation has no role in harsh environments. It is worth noting that Lortie & Callaway (2006) analyzed the above meta-analysis, exploring its general synthetic power, exposing severe limitations, and highlighting that the included studies were either not done along stress gradients, focused on invasive species, or were not peer-reviewed. Also, the stress gradients were

not identified nor quantified and also differed among studies. Furthermore, crucial sources of variation were not accounted for, either statistically or in the interpretations. The authors ultimately rejected the meta-analysis, reconfirming the validity of the SGH. However, more studies criticized the SGH validity in diverse situations. Casper (1996) evaluated the consequences of drought on the herbaceous perennial *Cryptantha flava* by analyzing plant density, plant size, and their association with shrubs, revealing that even under limited water presence in the soil, there was no evidence of any intraspecific competition or facilitation among the investigated plants. Pennings et al. (2003) assessed whether positive interactions, established among salt-marsh-plants at fine scales, can be extrapolated across broader geographic scales. Their results revealed the difficulty of inferring positive interactions from well-understood systems to dissimilar geographic locations or scales, concluding that selection effects on individuals and species may change the way populations react to varied environmental restraints. Tielbörger & Kadmon (2000) measured the influence of shrubs, in both direction and magnitude, on four annual desert plant species throughout four successive seasons with different rainfall quantities. Results revealed that their effect shifted from negative to neutral or neutral towards positive, with an annual precipitation increase. Another study in arid areas by Holzapfel et al. (2006) observed that with an increase in water availability, desert shrubs would have steady and consistent alteration from net positive or neutral effects to net negative effects on annual species. By assessing the demographic data from a population of the desert shrub *Ambrosia dumosa*, Miriti (2006) determined that both the direction and magnitude of facilitation may alternate during the ontogeny of the interacting species. This size-dependent ontogenetic shift occurs when nearby adult plants significantly improve the demographic performance of juveniles but reduce the effect of larger already established plants. Kawai & Tokeshi (2007) tested possible differences in the strength of the interaction patterns along the stress gradient, revealing that the transitions from competition to facilitation might be subject to the nature of the stress gradient involved.

Discussions and criticisms conforming with those previously mentioned paved the way even further forward via new scientific publications offering alternative models to the initially proposed SGH. Those new concepts proposed weakening and collapse of facilitation when climate change converse to either more benign conditions or under extremely stressful environments (Malkinson & Tielbörger, 2010; McCluney et al., 2012). Michalet et al. (2006) presented it as follows “diversity is

low in the least productive environments, highest at moderate levels of productivity, and then low again at very high levels of productivity” hence, reconfirming the conceptual model for the ‘humped-back’ pattern that was suggested initially by Grime (1973). Assessing the facilitation impact on shaping the community biomass–species richness, Xiao et al. (2009) showed that facilitation increased community richness when moving from medium to high environmental severity, but had a partial effect on population richness, not only in benign environments (high community biomass) but also at the harshest (low community biomass). Accordingly, facilitation decreases community richness from low to medium environmental severity. Where limited resources are the only fundamental abiotic stress factors, facilitation occurs when neighbors increase the availability of this resource (Maestre & Cortina, 2004). Although facilitation extends the range of situations where a plant can occur, Holmgren & Scheffer (2010) argued that positive interactions could be more evident in improving the performance of the species under moderately stressful environments rather than under extreme environments. Le Bagousse-Pinguet et al. (2014) suggested that a high level of restrictions caused by co-occurring stress and disturbance will obstruct the effects of plant interactions on species diversity, emphasizing their role in diversity regulation, along with the maintenance/extinction of plant populations. Michalet et al. (2014) revealed that in water-stressed ecosystems, facilitation would collapse or change to competition. A decline in the effect of the nurse plant species would collapse facilitation. However, environmental conditions along with the strategy of the response of the species would shift from facilitation to competition. This difference in SGH would help predict possible results when evaluating biotic interactions along stress gradients or during the restoration of a degraded ecosystem by using nurse species and their expected facilitation effects.

The preceded refinements of the initially proposed SGH theory were summarized by Brooker et al. (2008) in a highly cited publication. The publication, as its title indicates, “Facilitations in plant communities: the past, the present, and the future” covered various matters such as facilitation and environmental gradients, indirect interactions and facilitation, development of ecological models incorporating plant facilitation, relating facilitation to evolution, global changes, and ways of applying it in ecosystem restoration. Maestre et al. (2009) attempted to refine the SGH regarding competition and facilitation to enable predicting the complexity of possible outcomes when studying biotic

relations along stress gradients. The paper deduced two arguments: Facilitation is expected to upsurge with the stressfulness of conditions where the abiotic stress gradient is not determined by resource restrictions (e.g., temperature) or when the facilitated species is stress-tolerant. The hump-shaped model (with negative interactions nullifying facilitation at both ends of the stress gradient) is predictable, especially when the stress gradient is compelled by a resource (e.g., water), when both benefactor and beneficiary species have similar life histories (Brooker et al., 2008), or require same resources (Callaway, 2007).

Role of facilitation at the entire community level

Despite the well-documented effects of facilitation at both individual and population levels, facilitation at the community level has received much less attention (Cavieres & Badano, 2009). Competitive and facilitative mechanisms are not independent players in nature, occurring instead within the same plant community producing variable outcomes best comprehended when compared along different gradients such as abiotic stress, consumer pressure, sizes, and densities of interacting species (Callaway & Walker, 1997). Facilitation in plant communities increases under abiotic stress (e.g., temperature or salinity), ameliorating conditions for neighbor plants by influencing growths (Bertness & Callaway, 1994) and by increasing species diversity thru improving individual fitness (Hacker & Gaines, 1997) against physical stresses, predation, and aiding in nutritional transfer, trophic facilitation, and providing refuge from competition (Stachowicz, 2001). Moreover, the net outcome could alter during the different plant life stages in a community, for example, positive effects of benefactors when recipients are young vs. competition when beneficiaries are mature (Kellman & Kading, 1992). Interactions at the community level could also be indirect, occurring when a third species (or more species) alters the interaction between two other species (Connell, 1990), such as when the parasitic plant *Cuscuta salina* indirectly facilitates *Limonium californicum* and *Frankenia salina* by suppressing the competitive dominant plant *Salicornia virginica* (Pennings & Callaway, 1996). As previously mentioned, the humped-back relationship (Grime, 1973) reveals low diversity in the least productive environments and at very high productivity levels vs. highest diversity at moderate levels of productivity (Michalet et al., 2006). Assessing the effect of direct positive interactions on species diversity at the community level, Hacker & Gaines (1997) revealed that facilitation could shift the classical humped-back model by creating a

"compensatory mortality" zone at the left-hand side of the curve, preventing or ameliorating harsh conditions, physical disruptions, predations, among other stress types. These facilitative interactions at the community level are visible, for example, in harsh Alpine habitats where actions of cushion plants affect species abundance by creating plant groupings different from those found in open areas, ultimately increasing species diversity at the community level (Cavieres & Badano 2009). The concept of facilitation at community level could also be incorporated into the niche concept. The niche concept (Grinnell, 1917) is defined as a set of biotic and abiotic conditions in which a species can persist and maintain stable population sizes (Hutchinson, 1957). In a niche, neighboring species have negative impacts (or a niche-shrinking effect) on each other, firmly bounding to the competitive exclusion notion, where no two species can utilize the same niche (Higashi, 1993). Two types of niches exist, the fundamental and the realized niche. The fundamental niche is the abiotic conditions in which a species can persist in a range of environmental conditions in the absence of negative interactions such as competition, parasitism, and predation. Whereas the realized niche describes the conditions in which a species persists given the presence of other species (e.g., competitors and predators) (Hutchinson, 1957). Incorporating facilitation into the niche theory can impact it by modifying the relationship between the fundamental and realized niche (Bruno et al., 2003), making the spatial extent of the realized niche larger than the spatial range predicted by the fundamental one (Higashi, 1993; Bruno et al., 2003). Yet, Lucero et al. (2019) assessed 'the dark side of facilitation' by testing, in an arid ecosystem, whether native or exotic annuals are more facilitated by native shrubs. Results showed that facilitation by native shrubs toward exotic annuals was stronger than towards native annuals.

Main facilitation mechanisms

Ever since Aikman (1926) studied environmental alterations between sub-canopy and exposed microhabitats in deciduous forests of eastern Nebraska ecologists have documented several changes in microhabitat and multitrophic-level relations caused by plants facilitating the development and persistence of other plant species. Plant-plant facilitation could be divided into either direct or indirect mechanisms.

Direct Mechanisms for Facilitation

Field experiments demonstrated positive plant facilitation as abiotic stress modifiers (Walker & Chapin, 1986), including favorable modification of light, temperature, soil aeration (Callaway, 1995), soil nutrients, and soil moisture in semiarid environments (Holzapfel & Mahall, 1999).

Resource Modification

Light, shade, and temperature modification

In desert habitats, existing shades are a remarkable example of facilitative mechanisms within plant communities (Callaway, 2007). The shade of large plant canopies can shelter saplings and small plants from extreme temperatures by reducing their water loss (Callaway, 1995), thermal stress, and transpiration (Domingo et al., 1999; Moro et al., 1997a). Assessing the effect of the leguminous shrub *Retama sphaerocarpa* on the seedlings underneath it, Moro et al. (1997b) reported a drop of 60% in radiation compared to the exterior, registering a difference in temperature up to 7°C between inside and outside. In salty marshes, Bertness & Yeh (1994) observed that seedlings of marsh-elder plants (*Iva frutescens*) flourished best either in areas of high seedling density or where adult plants form a canopy. Reduced evaporation rates and increased shade ultimately decreased evaporation and soil salinity, shifting interspecific interaction from competition to facilitation (Bertness & Shumway, 1993). Nobel (1980b) affirmed facilitation by indicating a temperature drop up to 11 °C on the stem surface of *Ferocactus acanthodes* due to the effect of nurse plant shade. Even in winter, with low temperatures in the desert, the facilitative nurse canopies of *Cercidium microphyllum* mitigate cold temperature effects, consequently increasing apical stem temperatures of small saguaro cacti (*Carnegiea gigantea*) (Nobel, 1980a).

Soil moisture modification

Several factors play a role in the effect of plants on soil moisture, either positively or negatively, depending on various aspects such as specific plant architecture, physiology, or amount of rainfall per event (Pugnaire et al., 2011). Holmgren et al. (1997) highlighted contributing factors that lower water stress in the shade, consequently assisting seedling establishment in dry environments. Those factors are less transpiration, increase in soil moisture due to less evaporation, reduced salinity, enhanced water holding capacity, favorable conditions for root growth because of enhanced soil

structure and stability, elevated soil moisture, and lower soil temperatures, where the relative importance of these factors depending on individual ecosystems. Wied & Galen (1998) examined the effect of plants in facilitating conspecific seedlings through the enhancement of moisture conditions in alpine environments. Results showed that decaying plant material favored and preserved seedling establishment by protecting the underneath soil, establishing microsites with higher soil moisture, and lowering evaporation rates. Associating microclimatic conditions of tussock grassland on south-facing and north-facing slopes, Pålsson (1974) observed that on both slope aspects, relative humidity and temperature were similar within *Ononis repens* tussocks when compared to the less hospitable surrounding open matrix. Such an amelioration in microhabitat enabled certain herbaceous species common on the north-facing slopes to thrive on the south-facing slopes when associated with *O. repens*. Another mechanism of soil moisture modification by plant facilitation is water-lifting by deep-rooted species via the “Hydraulic lift” strategy (Richards & Caldwell, 1987), leading to significant consequences at the community scale. This passive water movement amongst plant roots with different water potential gradients lifts water from lower wet soil zones towards the upper dry soil surface (Prieto et al., 2012). *Retama sphaerocarpa* shrubs that hydraulically lift water have better water relations and growth rates when compared to those that do not have access to this water source (Prieto et al., 2011). Numerous plant-facilitating species such as *Artemisia tridentata*, *Larrea tridentata*, and *Ambrosia dumosa* are capable of water translocating from deep wet soils upwards toward dry soil surface to be used by other seedlings (Richards & Caldwell, 1987; Yoder & Nowak, 1999). Soil moisture and its relationship between water limitation and facilitation are one of the controversial debates surrounding the SGH. Butterfield et al. (2016) assessed this relationship by testing soil moisture in mediating plant-plant interactions along with climate and soil texture by simulating soil moisture dynamics under shrubs and in gaps using data from hundreds of sites in the western United States. Results indicated that when average conditions in the long-term were considered, the difference between soil moisture under shrubs and in the gaps decreased along the aridity gradient- conflicting SGH expectations. However, when considering extreme years, the positive effects of the shrub on soil moisture were the greatest at intermediate points along the spatial aridity gradient, consistent with the hump-backed model of plant-plant interactions (Michalet et al., 2006; Holmgren & Scheffer, 2010).

Soil nutrient modification

Soils beneath perennial species are usually more nutrient abundant when compared to those soils in adjacent open spaces with no perennial cover (Cortina & Maestre, 2005). This fact could be due to “nutrient pumping” (Richards & Caldwell, 1987), which involves the transfer of the nutrients of deep-rooted perennials to shallow-rooted species and indirectly depositing them on surface soil through litterfall and throughfall (Zinke, 1962). Airborne particles could also be trapped and deposited by the canopy of perennial at their base (Pugnaire et al., 1996; Whitford et al., 1997).

Soil oxygenation

Several plants species adapted to anoxic soils seem capable of ameliorating conditions for those less adapted plants by supplying oxygen which could leak out of underwater roots, oxidizing nutrients and toxic substances in the rhizosphere (Armstrong et al., 1992), oxygenating and aerating marsh sediments (Howes et al., 1981), ultimately, increasing the performance of coexisting plants (Bertness & Hacker, 1994).

Substrate Modification

Establishment of soil humus

Some perennial plants create “fertile islands” (Garner & Steinberger, 1989) or “resource islands” (Schlesinger et al., 1996) under their canopy. This is due to the accumulation of wind-blown soils and debris (Armbrust & Bilbro, 1997), facilitating the creation of suitable habitats for diverse organisms (Carrillo-Garcia et al., 1999), leading to increased decomposition, increase in soil nutrients level underneath (Gutiérrez et al., 1993), ultimately resulting in microclimate modification (Valiente-Banuet & Ezcurra, 1991), and enhancement of water availability (Callaway, 1997). In such islands, facilitation is usually the dominant interaction (Moro et al., 1997a).

Root grafts

Detected in more than 150 species, root grafts are common naturally among different plant species (Bormann, 1966), leading to resource sharing, like photosynthates, nutrients, water (Fraser et al., 2006), and secondary compounds among trees, challenging the classic competition concept (Begon et al., 2006), by increasing survival of suppressed trees (Fraser et al., 2006), lowering death rate of

mature trees (Tarroux et al., 2010), and even lowering hurricane damage among grafted trees (Basnet et al., 1993). In a root grafting study, Vincent et al. (2009) demonstrated that when root-grafted trees had their neighbors mechanically thinned resulted in stagnant and deteriorated trees.

Mycorrhizae and soil microbes

In severe environments, soil microbes and understory plants can form important positive mechanisms (Sylvia & Williams, 1992) that preserve plant biodiversity and ecosystem functioning (Rodríguez-Echeverría et al., 2013). Mycorrhizal fungi can support plant–plant facilitation through interconnecting plant individuals from varied species, genera, and even families in a community (Newman, 1988), through networks termed ‘wood-wide-webs’ (Simard et al., 1997). Arbuscular mycorrhizal (AM) fungi impact growth, expansion, and stability of the plant-soil systems of both roots and soil by enriching plant growth through nutrient uptake by soil fungi, leading to more interception of wind-borne soil, attached by mycorrhiza, leading to additional nutrients for the plant, and a growth substrate for the fungus, hence, closing the cycle (Carrillo-Garcia et al., 1999). With their hyphae, AM interconnects roots of neighboring plants (Allen & Allen, 1990), facilitating positive root exchanges between facilitators and facilitated plants, allowing the transfer of nutrients such as phosphorus (Smith et al., 2001), nitrogen, and carbon between leguminous and non-leguminous plants (Padilla & Pugnaire, 2006). AM can also have significant importance on seedling establishment, which through their attachment to the Mycorrhizal networks and Mycorrhizal roots of established trees leads to a lower mortality rate (Teste et al., 2009). AM can also improve nutrient absorption by the seedling even though its tissue is not fully developed (Kytöviita et al., 2003), permitting the establishment of a more fit and consistent plant (Magnusson & Magnusson, 1993). Mycorrhizal fungi can also aid in stress resistance, water uptake, and sometimes soil pathogens control (Augé, 2001; Sikes et al., 2009).

Indirect Mechanisms for Facilitation

Protection from herbivores

Facilitation by graze-resistant plants, also termed associational resistance (Bakker et al., 2004) or associational plant refuges (Pfister & Hay, 1988), is an essential facilitation process protecting plants from herbivores. Whereas saplings beneath, or next to, highly palatable shrubs could be more susceptible to herbivore grazing (Rousset & Lepart, 2003), beneficiary plants growing next to

unpalatable adult plants (Smit et al., 2006) have reduced chances of being eaten or trampled, since they could be protected physically or indirectly from herbivores (Baraza et al., 2006, 2007), consequently leading to an increase in plant size and reproductive output (Callaway et al., 2005). Thorns, unpalatable bushy twigs, or leaves may have a bigger effect than single standard stems (Flores & Jurado, 2003). The highly palatable *Whitania frutescens* is grazed exceedingly when not present alongside *Maytenus senegalensis* shrub—a plant with low palatability and full of thorns (Tirado, 2003). In a 10-year study, Olff et al. (1999) revealed that small unpalatable species (e.g., toxic, thorny, or of low quality) facilitate taller unpalatable shrubs, which in turn facilitate palatable trees, ultimately leading to shading the species that facilitated their recruitment. The study concluded that less-palatable tree species would favorably regenerate in open spaces, whereas more-palatable species would grow only amongst less-palatable shrubs—ultimately leading to an enhancement in community diversity.

Pollination

Pollination is crucial for plant reproductive success (Fægri & Van der Pijl, 2013). The term ‘magnet-species’ was coined by Thomson (1978) as a reference to attractive plant species that participate in increasing pollination of other species. Facilitation among plants occurs when a plant species facilitates pollination by indirectly increasing the number of pollinators visiting a second plant species, thus increasing its pollination rate (Feldman et al., 2004), even among invasive species (Molina-Montenegro et al., 2008). A yellow-flowered *Hietacium florentinum* was more pollinated when associated with the orange-flowered *Hietacium auranticum*, ultimately leading to an increase in seed output (Lavery, 1992). Pollinator-mediated facilitation exists not only within the same plant species but also among different species (Sargent & Ackerly, 2008), benefiting plants in small isolated communities the most (Groom, 1998). Hansen et al. (2007) noted that this indirect plant facilitation for pollination could alter during the same season and is most efficient during the highest bloom period.

Nurse plants - a promising facilitator?

What is a nurse plant?

‘Nurse Plant Syndrome’ is a specific type of facilitation that involves interaction between adult plants and seedlings. The nurse plant syndrome, also known as ‘nurse-protégé interaction’ (Cody, 1993),

was coined originally by Niering et al. (1963) to describe plants that have positive nursing effects on their seedlings under their canopy compared to seedlings found in the gap spaces outside. This effect creates a positive spatial association between seedlings of one plant, whether the same or, of different species, to a sheltering adult plant (Turner et al., 1966, 1969; Steenberg & Lowe, 1969, 1977). Nurse Plants may buffer non-optimal environmental situations, which could be essential in water-limited environments (Niering et al., 1963) by aiding in the interception of rainfall (Padilla & Pugnaire, 2006), improving abiotic stress conditions (Bertness & Callaway, 1994), ameliorating poor starting conditions, or sluggish growth due to extreme temperatures (Flores & Jurado, 2003). It can also aid through shade creation, consequently dropping thermal temperatures and reducing soil water evaporation (Domingo et al., 1999), cutting down radiation, shielding seedlings from the harmful effects of extreme temperatures, and lowering air moisture in arid environments (Pugnaire et al., 2011). Nurse plants could additionally reduce the frost effect (Padilla & Pugnaire, 2006), act as windbreaks (Walker et al., 2007), increase seed arrival and trapping (Giladi et al., 2013), and supply nutrients and stock water (Flores & Jurado, 2003). Nurse plants may also shelter seedlings growing beneath them against grazing (Padilla & Pugnaire, 2006) due to different morphological structures such as thorns, branches, and woody stems (Callaway, 2007). They could also physically protect understory plants from the trampling of grazing animals (Barbosa et al., 2009) via repulsion by secondary compounds (Bee et al., 2009) or reducing palatability (Smit et al., 2006). Nurse plants could also be highly attractive to pollinators by increasing their visits to the target plants (Padilla & Pugnaire, 2006), consequently increasing the pollination rate either to beneficiaries (Lavery, 1992) or with protected plants mutually benefiting from visits of shared pollinators (Moeller, 2004). Nurse plants can enhance soil fertility with the accumulation of higher litter and sediment quantities beneath them when compared to gaps (Rodríguez-Echeverría et al., 2016), positively modifying soil nutrients (Walker et al., 2001), increasing nutrient content (Callaway, 1995), and ultimately ameliorating the micro-climate when compared to nearby open areas (Pugnaire et al., 1996). It can also indirectly enhance soil chemistry for understory plants through mycorrhizal-colonization facilitation (Cuenca & Lovera, 1992) with a correlated upsurge in nutrient availability for such plants along with an increase in microbial abundance beneath them, leading to higher mineralization and availability of nutrients (Pugnaire et al., 1996; Moro et al., 1997a) for beneficiaries, accordingly, leading to facilitation (Rodríguez-Echeverría et al., 2016). By inhibiting one species, nurse plants may

help release other species from the competition (del Moral & Rozzell, 2005). Finally, a nurse plant should not release allelopathic or other harmful compounds to beneficiary ones (Padilla & Pugnaire, 2006).

Types and habitats of nurse plants

A meta-analysis study showed that woody species, predominantly shrubs (46% of total studies) (Filazzola & Lortie, 2014), are used as nurse plants in restoration practices (Gómez-Aparicio, 2009), alternating soil characteristics and micro-climate beneath them leading to the establishment of so-called 'fertile islands' (Garner & Steinberger, 1989), or 'resource islands' (Schlesinger et al., 1996). In some specific cases, a nurse plant could have a gender effect. A study on the dioecious species *Juniperus thurifera* trees acting as a nurse plant for saplings of its kind revealed that the establishment of most seedlings was under female trees because of perching birds on those female trees. The study concluded that the spatial structure of recruitment could be affected by nurse plant gender (Montesinos et al., 2007).

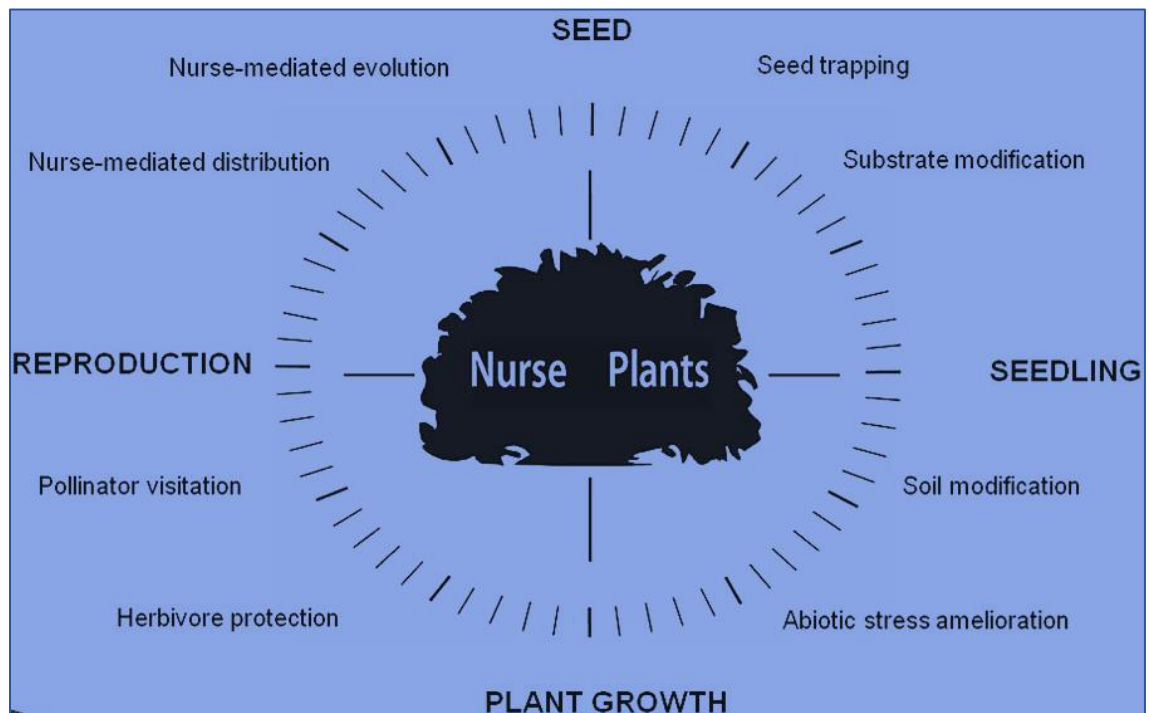


Figure L. 2. A theoretical framework for the biotic and abiotic mechanisms of nurse plant effects through their life (from Filazzola & Lortie, 2014).

Filazzola & Lortie (2014) reviewed 298 articles on nurse-plant interactions based on geographic region, facilitation mechanism, ecological hypothesis, and nurse life form. Results showed that the

majority of the studies of positive plant interactions were most frequent in areas of high abiotic stress (11.7% in a Mediterranean climate-18.6 % in the Arctic and Alpine climates-43.6 % in arid and Semiarid climates). Accordingly, nurse plants exist in a wide range of habitats ranging from alpinos (Cavieres et al., 2002; Nuñez et al., 1999), deserts (Franco & Nobel, 1988; Tielbörger & Kadmon, 2000), wetlands (Egerova et al., 2003), salt marshes (Bertness & Hacker, 1994), grasslands (Greenlee & Callaway, 1996), tropical woods (Guevara et al., 1986), savannas (Archer et al., 1988), and Mediterranean habitats (Verdú & García-Fayos, 2003).

Filazzola & Lortie (2014) Illustrated a theoretical framework for the biotic and abiotic mechanisms of nurse-plant effects investigated in the literature, noting that nurse mechanisms could affect protégés through their life commencing from seed germination until reproduction passing through saplings and throughout all other growth stages (figure L. 2).

Semiarid Mediterranean environment habitats

Challenges and hopes

Human impacts in the Mediterranean Basin

The Mediterranean Basin (MB) has a unique character resulting from geographic, historical conditions, and social developments (Ruti et al., 2008). Although covering only 2% of the Earth's total area, the basin globally ranks third among hotspots in plant diversity and endemism behind the Tropical Andes and Sundaland (MoE/UNEP/GEF, 2016). With faulted and folded limestone (creating scattered and fragmented hotspots)(Médail & Quézel, 1999), several highly differentiated biogeographical patterns at varied elevations ranging from sea level up to alpine (Vogiatzakis et al., 2006), and various land-use practices in space and time, the MB by itself (Figure L. 3.) offers a variety of habitats resulting in a large number of endemic plant and animal species, accordingly, it is considered as one of 34 worldwide identified biodiversity hotspots (Médail & Quézel, 1997). Its flora comprises up to 25,000 native plant species, of which more than half (13,000 plants) are endemic (Myers et al., 2000) and 18.24 % threatened (Calow, 2009), forming about 80% of all European and 8% of world flora (Valavanidis & Vlachogianni, 2011). Summer drought, air temperature, and winter rainfall, typical features of the Mediterranean Basin climate, are critical ecological factors bounding

an active growing season between the wet fall and spring period of the year (Blondel & Aronson, 1999). This diverse region of towering mountains, woods, ancient rivers, deserts, and thousands of islets, is the stage where both civilizations, dating back thousands of years, and wild nature coexisted to create a mosaic of natural and cultural landscapes (Mannion, 1999; Cuttelod et al., 2009), ultimately, generating original ecosystems and landscapes with unique biodiversity (Dutoit, 2010). This biodiversity has been shaped and reshaped by humans for almost 10,000 years (Pons & Quézel, 1985) through the immense impact of the successive rising and falling of civilizations over several millennia on biota and ecosystems everywhere in the basin (Blondel, 2006), sequentially, shaping the Mediterranean region as unique in world bioclimatic regions (Naveh & Carmel, 2004). Whether this human impact has benefited or was damaging to the Mediterranean biodiversity is debatable, leading to the development of two opposing theories. The first is the 'ruined landscape' or 'lost Eden' theory promoted by Attenborough & Wright (1987), suggesting that various human actions, such as overgrazing and deforestation, lead to progressive and cumulative degradation and desertification of the Mediterranean landscapes. Whereas an opposing theory claimed a positive contribution by humans in preserving Mediterranean landscapes favoring varied biodiversities by influencing a variety of cultural landscapes (Grove & Rackham, 2001; Blondel, 2006). With either of the two proposed theories, the fact remains that the MB has had an incredible chain of diversity. Numerous civilizations (Mesopotamian, Egyptian, Phoenician, Jew, Greek, Roman, and Arab) have affected biodiversity by shaping a variety of cultural landscapes throughout eras of severe pressure through practices such as terracing, grazing, cutting, burning, clearing, and cultivating arable areas (Pausas et al., 2008), have ultimately contributed to the current landscape (Zavala & Burkey, 1997). Unfortunately, in the process, significant disruptions were caused by numerous factors such as habitat loss, degradation, over-exploitation, pollution, natural disasters, invasive alien species, and severe human disturbances (Cuttelod et al., 2009). All have had a direct impact on the basin due to its very low resilient capacity in facing such major disruptions (Dutoit, 2010). This influence of humans on biological systems in the MB has been so profound and widespread, leading to an 'anthropogenic' structure of plant communities (Naveh & Kutiel, 1990), considerably affecting forest structure and composition (Blondel & Aronson, 1995; Grove & Rackham, 2001). Altering Mediterranean habitats has accelerated remarkably during the last two centuries rendering them severely fragmented or destroyed primarily as a result of urbanization, industrialization, and tourism

activities (EEA, 1999). Intense land-use alterations profoundly affected most Mediterranean landscapes (Lepart & Debussche, 1992) by impacting biodiversity and other ecosystem services of the region due to various human pressures such as climate change, land degradation (Scarascia-Mugnozza & Matteucci, 2012), air pollution- mainly in the form of nitrogen (N) deposition, tropospheric ozone (O₃), and particulate matter (Paoletti, 2006; Ferretti et al., 2014). Another major affecting factor, in several semiarid Mediterranean areas, is erosion, a problem that is likely to increase under swelling land-use changes and flood recurrences (Terrado et al., 2014).

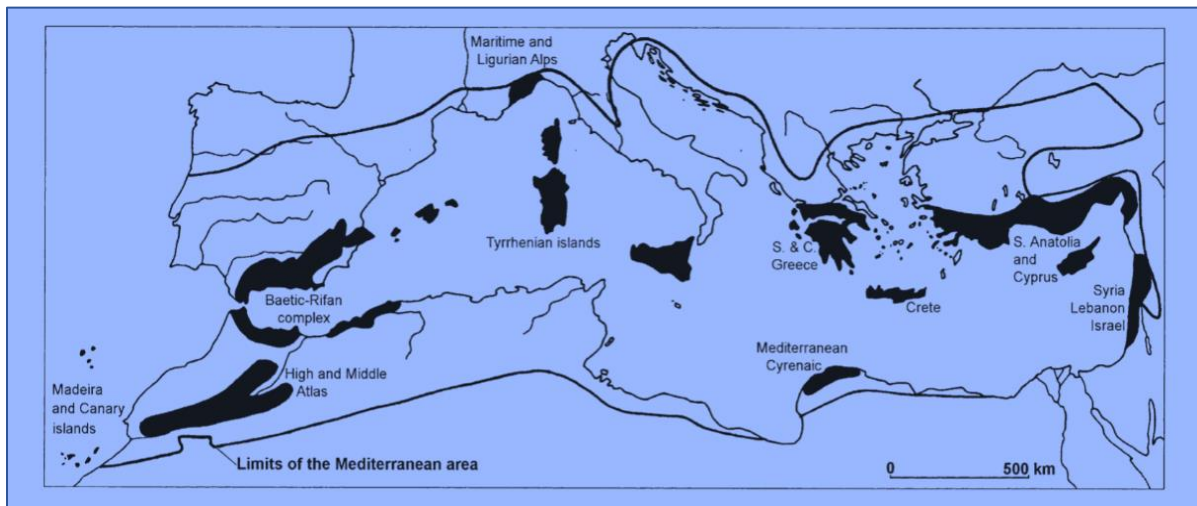


Figure L. 3. Biodiversity hotspots in the Mediterranean Basin (from Medail & Quézel, 1999)

Ecological restoration, history, and practices in the Mediterranean Basin

Ecological restoration is generally a challenging task under stressful circumstances of the Mediterranean drylands (Cortina et al., 2011). Some of those challenges include (1) Defining appropriate models of vegetation dynamics to be used as reference (such as natural, historic,...), (2) The need for a profound understanding of abiotic and biotic factors affecting ecosystem functioning, (3) Promotion of better ecological restoration governance based on wider social participation and diffusion networks, and (4) The need for better quality control for the evaluation of scientific projects (Mucina et al., 2017). Historically, restoration ecology in the Mediterranean Basin started in the mid-nineteenth century, when several countries- extensively France and Spain- carried out afforestation programs. These plans, described as simple ecological restoration practices, aimed to protect the watershed and headwater areas, regulate stream flow, reduce flash floods, control soil erosion, and

provide forest products (Vallejo et al., 2012). Those practices progressed into the twentieth century through several restoration projects conducted across the Mediterranean Basin during its first half. Most performed projects had a silvicultural approach, which embraces planting fast-growing tree species (Nunes et al., 2016) while addressing a few broad restoration aims, such as soil erosion reduction, water runoff, or forest recovery (Vallejo et al., 2012). Unfortunately, and in most cases, the projects were monoculture tree stands of low biodiversity. Gradually, those practices were pursued later by more suitable ecosystem-based strategies centered on increasing plant species diversification and allocating more care for the fauna and soil preservation (Nunes et al., 2016). During the last quarter of the twentieth century, socioeconomic changes in southern Europe shifted the social demands placed on wildlands. Accordingly, new restoration goals emerged (Bautista et al., 2010) with new objectives conducted within the framework of various projects and purposed to prevent wildfires, improve silvopastoralism, increase recreational and cultural wildlands use, and increase biodiversity - all administered simultaneously besides recovering native woodland ecosystems (Vallejo, 2009). Towards the end of the twentieth century and into the twenty-first century, to cope with the uncertainty induced by climate change (Stephens et al., 2010) with an expected temperature upsurge between 2-4 °C in the Mediterranean basin (Palutikof & Wigley 1996), ecological restoration efforts steered towards mitigating global warming and climate change, through the improvement of ecosystem resistance and resilience as principal universal objectives in restoration programs (Bautista et al., 2010). Practically successful restoration techniques in the Mediterranean Basin should include procedures adapted to the plant phenology of the region and the local Mediterranean climate. Such practices would embrace seeding, transplanting, hay transfer, and timely soil transfer (Buisson et al., 2021), to be applied in parallel with proper human-land management, including appropriate grazing and pastoral fires (San Miguel, 2008).

Lebanon, a multi-challenging environment

Location and importance as a hotspot

Due to its location, topography, and altitude (MoE/ECODIT, 2002), Lebanon's highly diverse ecosystem is considered a biodiversity hotspot in the MB (Myers et al., 2000). With heterogeneity in ecological forces affecting the evolution of its diversity (Dagher-Kharrat et al., 2018), Lebanon has approximately 9,116 known species divided into 4,486 species of fauna and around 4,630 species of

flora (MoA/UNEP, 1996). One of the most extraordinary characteristics of Lebanon is the presence of such biodiversity in a very restricted area of land- as Lebanon covers 0.007% of the world's land surface area and has about 0.8% of the world's species (MoE/UNEP/GEF, 2016). Relative to its size, Lebanon has one of the highest densities of floral diversity in the Mediterranean basin (Médail & Quézel, 1997), evident in terms of the very high species-area ratio of 0.25 species/km² (e.g., Brazil's species-area ratio is 0.0044/km² and South Africa's species-area ratio is 0.0081/km²) (MoE/UNDP/ECODIT, 2011). Despite centuries of deforestation and dwindling forest cover, floral richness is still high, probably due to the soil and bedrock structure, altitudinal variations, and difficulty of access (Khater & El-Hajj, 2012). The floristic richness is estimated to be around 2600 plant species, of which 12% are endemic (MoE/UNDP/ECODIT, 2011), divided between 221 broad endemics and 90 narrow endemics (MoA/UNEP, 1996). This high endemism is due to the isolation effects encountered on the high peaks of the Lebanese Western and Eastern Mountain Chains (Sattout & Abboud, 2007). However, for millennia, Lebanon's ecosystems have experienced significant changes, such as historic deforestation, widespread replanting, reforestation plans, bench terracing, recent civil war (1975–1991), unplanned urbanization (Faour, 2015), the inflow of refugees from nearby war-torn Syria (2011–2017) increasing its population by 30% (Ammar et al., 2016), and the escalating climate change crisis (Khater & El-Hajj 2012). The main threats to Lebanon's biodiversity could be summed as follows: Habitat loss and fragmentation, unsustainable exploitation of natural resources, pollution, invasive species, the introduction of new and improved varieties (agrobiodiversity), climate change, and the lack of data (MoE/UNEP/GEF, 2016). In recent times the multidimensional poverty rate in Lebanon (doubling from 42% in 2019 to 82% in 2021, dramatically increasing from less than 29% a few years earlier), deemed to be a major driving factor for people to behave in an unsustainable manner to suffice their survival needs (UNDP, 2018; <https://www.unescwa.org/publications/multidimensional-poverty-lebanon-2019-2021>). As a closing note, it is worth mentioning that the cost of environmental degradation linked to land and wildlife resources per year is estimated at \$100 million, equivalent to 0.6% of Lebanon's GDP (Sarraf et al., 2004).

Quarries in Lebanon

Situation

Lebanon's quarrying sector is notoriously uncontrolled and disorganized devastating environmental resources and landscape via numerous causes, including the rising demand for construction aggregates, political disputes, and delays in declaring quarry master plans (MoE/UNDP/ECODIT, 2011). Although the actual number of quarries on the Lebanese territory is variable (depending on the source of information), there are approximately 1,300 quarries dispersed all over Lebanon, causing horrendous damage to existing arable lands, accelerating erosion processes, modifying ecosystems, destroying natural habitats, interrupting natural successions, and changing landscape patterns (Khater et al., 2003; Khater, 2004). Up until 1996, quarries in Lebanon were controlled by Decree 235, issued in 1935 during the French mandate period (Leenders, 2012). During post-war reconstruction, in the 1990s, the very high demand for building materials (stones, sand, wood, etc.), led to the proliferation of quarries throughout Lebanon, with their number almost doubling between the years 1996 to 2005, from 711 to 1,278. This upsurge increased excavated land by 84% (from 2,873 to 5,283 ha), destroying 738 ha of grasslands, 676 ha of arable lands, and 137 ha of forest areas (Darwish et al., 2010). The World Bank in 2009 investigated the cost of environmental degradation from quarries, estimating it at \$34.5 million based on the Lebanese GDP of \$34.5 billion (WB, 2010). A long-awaited national master plan for quarries was declared in 2002 and later modified twice in 2006 and 2009 (Decree No. 5616/1996, Decree No. 8803/2002, Decree No. 16456/2006, Decree No. 1735/2009).

Previous successes and failures in quarries rehabilitation in Lebanon

Lebanon has several regulations concerning the quarry sector, with the most-important decrees affecting quarrying from 1996 to 2009. Unfortunately, the vast majority of the 1300 quarries are unlicensed or with an expired licenses. Few quarries have been undergoing rehabilitation, and fewer of which are even documented (Qaraoun state quarry, Sibline) (MOE/UNDP/ECODIT, 2011), and others are in process (Holcim Ciment Blanc, Mdoukha, and Aita el Fokhar quarries).

Maqneh quarry: history, location, site details

The quarry considered for this study is in the vicinity of the village Maqneh, in the middle of the Beqaa Plain, in east Lebanon. The plain, characterized by an approximate 10 km wide depression

separating the major two Lebanese mountain chains, the Western Mountain Chain and its Eastern Mountain Chain counterpart, is distinguished by a flat terrain that slopes gently at a less than 5 degrees/ km gradient. The long-abandoned quarry rests at the end of the rocky valley, where a seasonal stream (Wadi Nahle) exists with a U-shape cross-section indicating an old stage of maturity (Figure L. 4.).

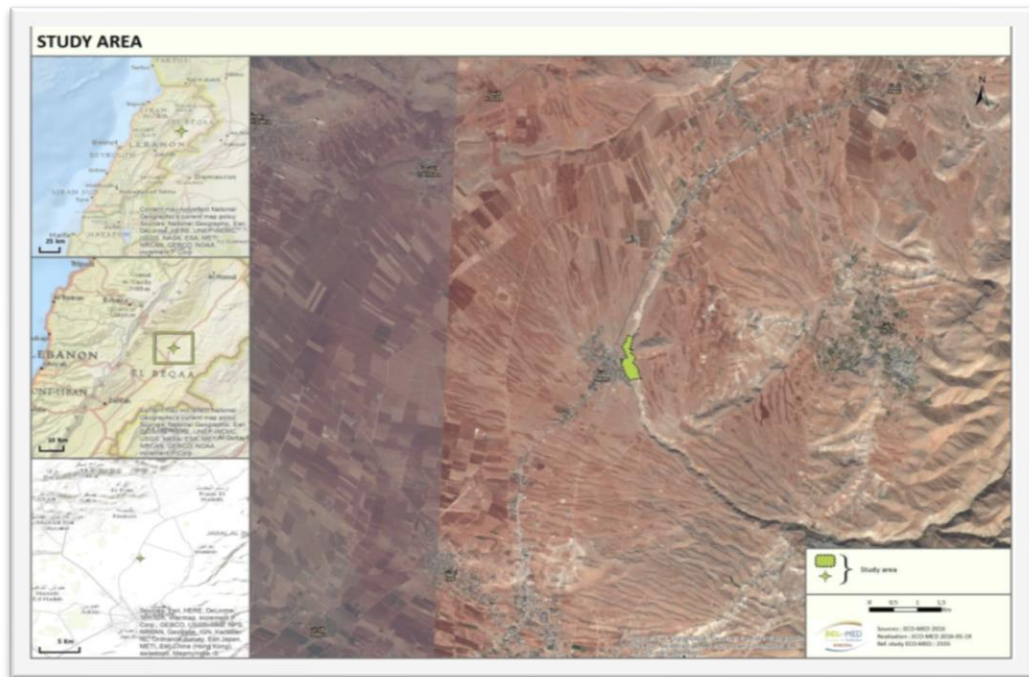


Figure L. 4. Location of the study area- Beqaa plain in Lebanon (modified from Ecomed).

The quarry itself consists of two main sides facing each other. One side is almost intact, consisting of natural cliffs and former old cultivated terraces not damaged by quarrying, embracing an array of native vegetation but overgrazed by sheep and goats for decades (Figure L. 5., Figure L. 6.).



Figure L. 5. The intact side of the quarry consists of natural cliffs and former old cultivated terraces not damaged by quarrying and embracing an array of native overgrazed vegetation. (Shaiban, IMBE).



Figure L. 6. Another angle of the intact side of the quarry consists of natural cliffs and former old cultivated terraces not damaged by quarrying and embracing an array of native overgrazed vegetation. (Shaiban, IMBE).

Whereas on the opposite side, the quarry stands up with its working face (Figure L. 7., Figure L. 8.).



Figure L. 7. The quarry side consists of severely degraded areas due to quarrying. (Shaiban,IMBE).



Figure L. 8. Another angle of the side of the quarry shows the impact on soils and vegetation. (Shaiban, IMBE).

From a Lithological perspective (Figure L. 9.), the quarry is characterized by a Cenomanian-Turonian Rock Formation (C4-5), of mainly reefal limestone, dolomitic limestone, and some dolomite inclusions situated next to another rock formation with marly facies, in which the latter is attributed to the Senonian Formation (C6). It is worth noting that a major fault isolates carbonate rocks from adjacent marls.

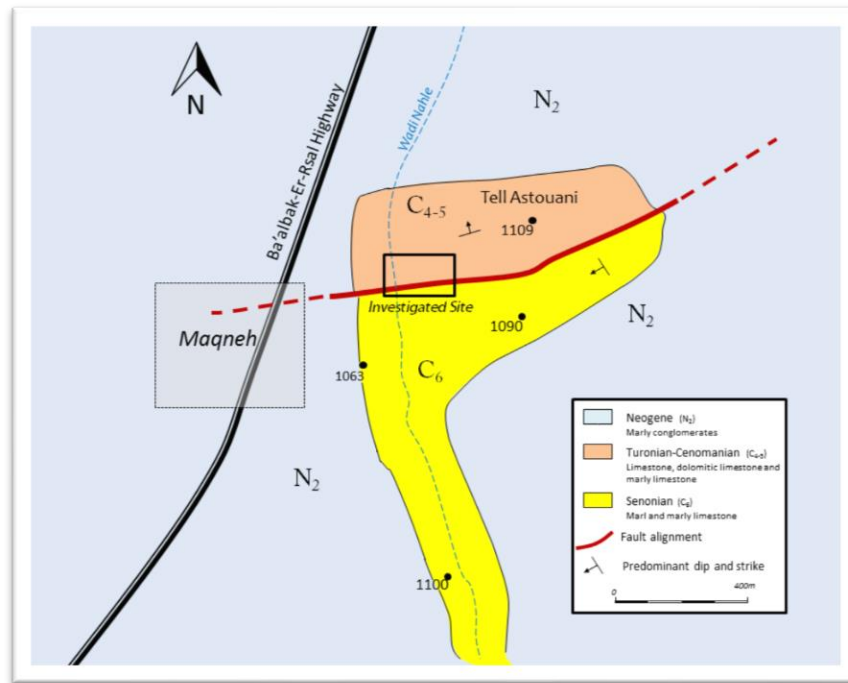


Figure L. 9.: Geologic map of the abandoned quarry locality in Maqneh and the surrounding (Maqneh Report- CNRS)

The site is within the Pre-Steppic Mediterranean Vegetation type ensemble encompassing the eastern slopes of the Mount Lebanon chain, the western slopes of the Anti-Lebanon range (both in their northern parts), and the plain extending between them (MoA/UNEP, 1996). In Lebanon, the vegetation type is categorized into four “vegetation levels”: The Pre-steppic Mediterranean, Pre-steppic Supramediterranean, Pre-steppic Mountainous Mediterranean, and Pre-steppic Oromediterranean. The study site belongs to two vegetation levels the Pre-steppic Mediterranean and Pre-steppic Supramediterranean.

The local flora in the surrounding natural habitats of the quarry can be considered highly rich with different plant species. Among them are some endemics (*Campanula euclasta*, *Stachys nivea*, *Alcea damascene*, *Astragalus roussaeanus*) along with species specialized to rocky habitats and slopes

(*Serratula cerinthifolia*, *Convolvulus dorycnium* ssp. *Oxysepalus*, *Capparis spinosa* ssp. *Parviflora*, *Parietaria judaica*, *Alkanna orientalis*, *Hyoscyamus aureus*, *Moluccella laevis*) that could be interesting in ecological restoration for their resilience actions (ecosystem healing and regeneration). (Rehabilitation Concept report for the Maqneh Quarry – Beqaa plain- Lebanon- CNRS- Lebanon). The vegetation has been (and still is) overgrazed for centuries by uncontrolled itinerant grazing sheep and goats, leading to a decrease in species richness, diversity, and alteration in species composition of surrounding grasslands. Unfortunately, no data or experiments have previously been done to exclude ungulates through fenced areas.

METHODOLOGICAL APPROACH

Why in an ex-situ mesocosm setting, and what are its limitations?

The composition, structure, and dynamics of plant communities are shaped primarily by interactions amongst plants (e.g., Gleason, 1917; Grime, 1998; Grace, 2012; Tilman, 2020). Nonetheless, establishing conclusive outcomes of such interactions under field conditions is time-consuming and proved to be a difficult task (Connell 1990), and could require enormous time to execute, lacks control over various external factors, and has an increased strain on examining effects of different components (Kulmatiski & Kardol, 2008). Therefore, in some particular cases, simulated communities developed within a greenhouse context are considered a more lenient approach (Gibson et al., 1999), offering several practical advantages over field-based experiments. Some of those advantages are, better control of treatments and extrinsic factors (Gibson et al., 1999), adequate evaluation of different factors like soil productiveness, the influence of pathogens, and herbivore effect (Keddy, 1989), add to this, such studies permit mechanistic analysis, rather than plain phenomenological surveillances (Stiling, 1992). Although ex-situ studies are effective tools in studying and conserving plants (Antofie, 2011), they might have several disadvantages, such as the tendency to simplify ecosystems (Jackson et al., 2005), neglect of the importance of understanding plants' ecological conditions, absence of the in-situ requirements of having varied and complex interactions among studied plant species (Wangalwa et al., 2021).

The competition index used, means of calculation, and its limitations

Of the various interactions amongst plants, competition is considered one of the major factors shaping and assembling plant communities (e.g., Grime, 2006; Keddy, 1989). Keddy et al. (2002) summed up several research questions and paths engaged in assessing competition amongst plants, correlating each with a different group of specific inquiries: (1) What is the effect of competition on plant distribution along gradients? (2) How does competition influence the coexistence of similar species? (3) What is the significance of competitive responses and effects? (4) How to analyze the

presence of competitive hierarchies and explore their patterns? (5) What are the means of inspections of the various plant traits and their presumable role in defining competitive performances? In this study, the research path followed was the fifth pathway, where competition is considered through the possible roles of plant traits in determining competitive performance (e.g., Tilman 1982; Gaudet & Keddy 1988; Keddy et al. 2002). Gaudet & Keddy (1988), in an original experiment using a comparative approach, i.e., “the systematic screening of a large number of species under standardized experimental conditions” (Grime & Hunt, 1975), to assess the relative competitive performance of wetland plant species by examining whether there was a correlation between the competitive performance and various plant traits. Their results revealed a strong correlation between the relative competitive performance and above-ground biomass, whereas other traits like plant height and canopy area interpreted the residual variation.

Numerous indices have been utilized to assess the net balance among plant interactions to determine whether competition or facilitation prevails in plant-plant interactions. These included the relative competition index (RCI) (Wilson & Keddy, 1986), used to measure diffuse competition, the relative neighbor effect (RNE) (Markham & Chanway, 1996), and the log response ratio (lnRR) (Hedges et al., 1999). Armas et al. (2004) proposed an index with strong mathematical and statistical properties that could potentially overcome several problems of other indices- the RII index, highlighted as “.... the most suitable index for analysis of plant interactions. RII has defined limits, it is symmetrical around zero with identical absolute values for competition and facilitation, its sampling properties are known and accurate, and it is safe to use in statistical and mathematical operations because it is linear and does not have discontinuities in its range”. RII has been utilized in various research areas to study the net balance of plant interactions, such as in arid regions (Holzapfel et al., 2006), in testing the severity-interaction relationship (SIR) (Elmendorf & Moore, 2007; Tirado & Pugnaire, 2005), in testing plant–plant interactions under grazing pressure (Howard et al., 2012), and in studying interactions between invasive plants and native species (Gao & He, 2014). RII was also used in drylands to assess the role of nurse successional stages on species-specific facilitation (Fagundes et al., 2018), in valuing Arbuscular Mycorrhizal Fungal intervention with respect to Plant-Plant interactions (Zhang et al., 2014), in studying soil origin and its microbes (Siefert et al., 2018), evaluating plants interactions interceded by salinity stress (Zhang et al., 2008),

assessing competitive effect between invasive and native wetland plant species (Hager, 2004), measuring direction and intensity of root interactions and their change with temperature (Luo et al., 2020), and in quantifying the effect of nutrients on plants such as Phosphorus (Zhang et al., 2016), and nitrogen (Matallana et al., 2017).

Although several reviews positively highlighted results generated by the RII index, some reported a few limitations with such a comparative approach. Keddy et al. (2002) noted two principal limitations, (1) its liability to only utilize one or a few reference species to rank other species, and (2) the fact that one or a few standardized environments are studied simultaneously. Díaz-Sierra et al. (2017) also noted that RII tends to underestimate facilitation with respect to equivalent values of competition.

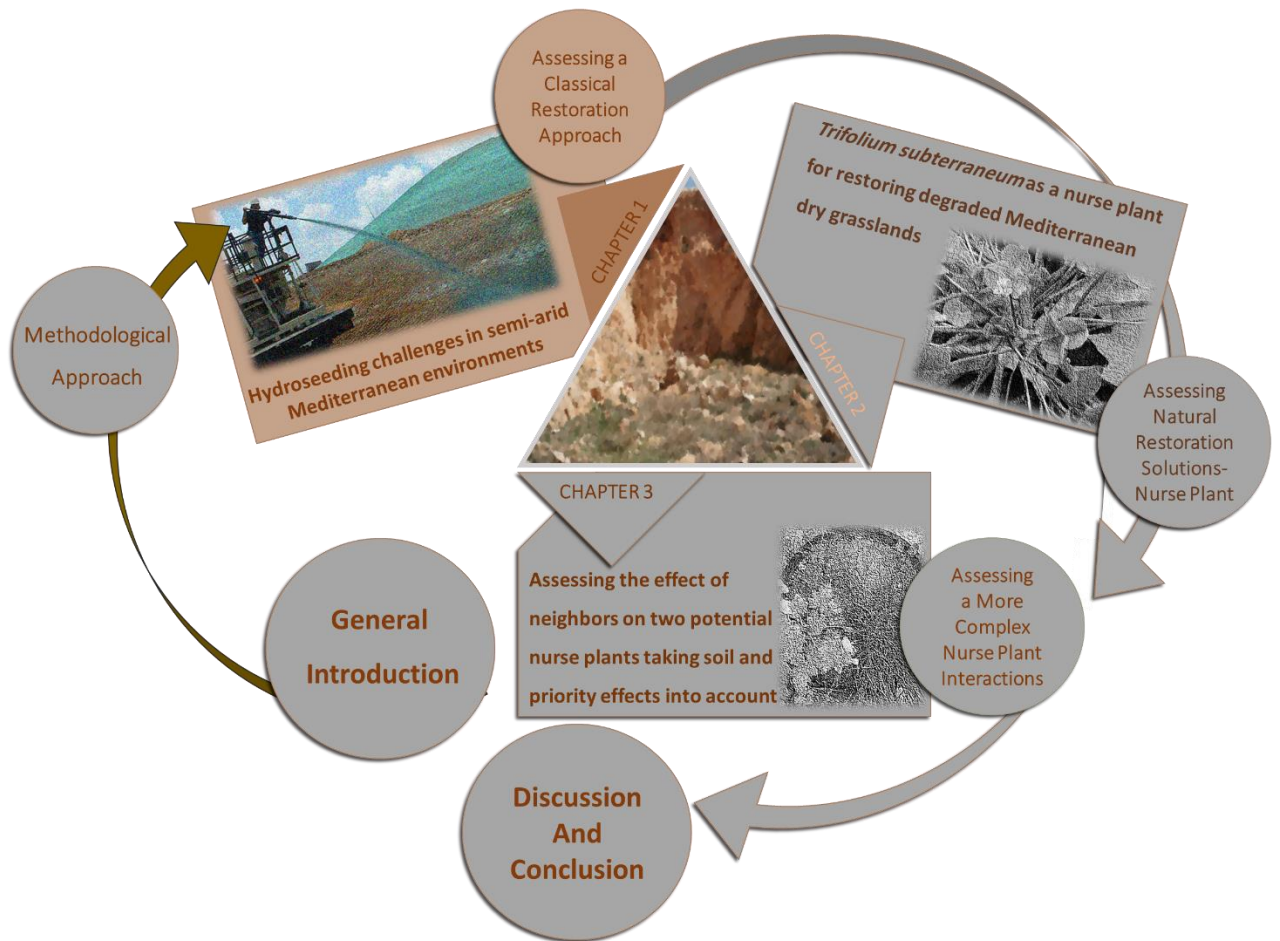


Figure M. 1. Location of chapter one in the general organization of the thesis.

CHAPTER ONE

Hydroseeding for Restoring Degraded Semi-Arid Mediterranean Environments: A Review of Challenges

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Abstract

Hydroseeding is a restoration technique commonly used in varied restoration projects. This literature review, encompassing about 100 published research papers from 1990 to 2020, revealed numerous limitations in a semiarid Mediterranean environment. Challenges facing hydroseeding as a restoration tool in semiarid Mediterranean environments were evaluated by analyzing different factors affecting ecological and technical levels. This issue was approached by sorting variables under either biotic or abiotic factors, further subdividing them under either natural-environmental or human-influenced factors. The review highlighted several constraints when applying hydroseeding techniques in a semiarid Mediterranean environment: Slope steepness, slope aspect, high water runoff, low presence of water, mixing solutions used, and high cost of applying this technique are some of those constraints facing its success. Other shortcomings are related to the low success rate of commercial seed mixtures under harsh conditions and their tendency to compete with native species. Moreover, the review provided recommendations to increase hydroseeding success by using varied techniques such as topsoil spreading, utilizing native seeds, mycorrhizal or rhizobium inoculation, and the use of nurse plants. Furthermore, an environmental psychology approach was suggested as means to convey a better message and increase acceptability towards improved innovative suggestions.

Keywords: Abiotic factors, biotic factors, limitations, success, failures, restoration techniques.

Introduction

Vegetation is a cornerstone of natural ecosystems. It is not only an essential habitat for different living species but also carries ecosystem services and functions such as nutrient cycling, soil protection, water purification, etc. (Hölzel et al., 2012). Numerous factors lead to ecosystem degradation and surface modifications with irreversible loss of soils via removal of upper soil, sedimentation, salinization, etc. Whenever a certain threshold level is crossed, it cannot reverse back without interventional correction to alternate what led to that threshold being crossed (Aronson et al., 1993). This fact is especially valid for semiarid Mediterranean ecosystems, where natural recovery after the disturbance has been recognized to be harder than in other ecosystem types (Blondel et al., 2010). In such conditions, ecological restoration techniques are required to initiate, assist, and accelerate the recovery of degraded ecosystems with respect to their structure, functional properties, and exchanges with surrounding landscapes (SER, 2004). Restoration is not easy and straightforward because of several factors restricting its success, such as abiotic and biotic constraints (Bakker & Berendse, 1999).

One important restoration technique applied to reintroduce vegetation is manual seeding, where seeds are hand spread with no specialized equipment. Such a manual method is suitable only for small areas (MacDonald et al., 2015). Drill seeding is another practice that involves seed application, utilizing conventional agricultural equipment below the soil surface. This practice is limited to relatively flat and well-groomed sites (MacDonald et al., 2015). Hydroseeding is another commonly used technique (Figure 1. 1.), especially on steep slopes and inaccessible regions (Davy, 2002). The process consists of mixing cellulose fiber, mulch, seeds, and later adding water into the tank and spraying the degraded area (Martin et al., 2002). Although used worldwide (more than 12 million km length of road networks in the United States, Europe, Japan, and Australia- Mola et al., 2011), hydroseeding has variable outcomes.



Figure 1. 1. Utilizing the hydroseeding technique as a restoration tool on a steep road cut slope

(Martin et al., 2002).

The Mediterranean region (Figure 1. 2.) covers about 850 million hectares in 22 countries across Southern Europe, the Middle East, and North Africa (Zdruli, 2014). In this vast region, hydroseeding as a restoration tool is increasingly applied (Andrés et al., 1996; Albaladejo et al., 2000; Matesanz et al., 2006; Tormo et al., 2007). A study from around the Mediterranean Basin, spanning over sixteen countries, surveyed 36 implemented restoration projects revealing that 17% of the total executed restoration projects were undertaken through hydroseeding practices and were carried out on post-industrial sites (mining), infrastructure development, deforestation, and drought sites (Nunes et al., 2016). In several cases, poor results in plant performance have been measured (Matesanz et al. 2006). Several direct and indirect variables determine the effectiveness of hydroseeding in semiarid Mediterranean environments. This

assessment should cover varied factors such as soil conditions, topography, season, climate, vegetation types, water availability, vulnerable or sensitive surrounding areas, and maintenance requirements. Once identified, those factors could be manipulated to improve restoration efforts (Tormo et al., 2008).



Figure 1. 2. The Mediterranean Basin with its 22 bordering countries (Modified from Google Maps)

Successful restoration results from a combination of ecologically sound projects that are technically possible, financially feasible, and socially acceptable (Khater, 2015). Hölzel et al. (2012) distinguished various factors affecting ecological restoration under three major headings: starting conditions, abiotic factors, and biotic factors.

This paper presents a review of more than 100 research papers published between 1990 and 2020, reporting the success and failure of hydroseeding as a restoration technique for large-scale projects. It analyzes the reported cases in view of biotic and abiotic factors

potentially affecting restoration success and differentiates between nature-based and human-related variables.

Methods

The different variables affecting hydroseeding successes and failures in a semiarid Mediterranean environment were assessed by exploiting diverse search engines (Google Scholars, Web of Science, Summon 2.0), searching in the title, abstract, and keywords of papers the following terms: “hydroseeding” plus “semiarid Mediterranean environment” plus “cultural practices”, “microclimate”, “nurse plants”, “seed type/ competition/ inoculation”, “slope aspect/ steepness”, “soil addition/ mulching”, or “mixing solutions”(See Table 1. 1.).

Results

Hydroseeding techniques and their limitations

In semiarid Mediterranean climates, hydroseeding has yielded poor results in plant performance (Matesanz et al., 2006). These results could be due to a lack of sufficient knowledge about the success of hydroseeded species and the performance of native species (Bochet & García-Fayos, 2004). Understanding the response of those established species is critical for successful ecosystem restoration and improving seed mixtures (González-Alday et al., 2008).

Several factors affect hydroseeding successes or failures. Those factors can be grouped under abiotic factors or biotic factors (Table 1. 2.). Starting conditions are the existing conditions ranging from abandoned semi-natural environments to areas intensively used as cropland or heavily disturbed places such as quarries and mines (Hölzel et al., 2012). Although it is a very important aspect, this topic will not be covered in this review because it is out of scope when discussing hydroseeding’s pros and cons.

Abiotic factors affecting hydroseeding

Numerous abiotic factors might affect the hydroseeding end result, those can either be natural-environmental factors or human-influenced factors (Table 1. 2.). Those factors do not act alone and often interact with one another or with different biotic factors.

Natural-environmental abiotic factors affecting hydroseeding

Natural-environmental abiotic factors are factors related to site topography, aspect, edaphic characteristics, and water availability. Topography and extreme environments can determine the success of a planting and restoration program (Bochet et al., 2009). Slope steepness, aspect, and type are all factors to consider in a harsh semiarid Mediterranean climate. Because of low penetration and high runoff (Miyazaki et al., 1993), slopes with steep angles have intense water insufficiency, which leads to very low plant cover, accentuating the difficulty of re-vegetating them (Andrés et al., 1996). Studies on motorway slopes in Catalonia-Spain concluded that hydroseeding was unsuitable for slope stabilization of road cuts near, or above, 45 degrees. The causes of failure include the probability of seeds moving downhill, with or without water (Cerdà & García-Fayos, 1997; García-Fayos & Cerdà, 1997). Even at lower steepness, on slope angles greater than 27–32 degrees, seed establishment is hindered by downward dragging (Bochet & García-Fayos, 2004). A study conducted in Malaga-Spain assessed whether hydroseeding techniques had any significance to contribute to species richness and vegetation cover by acting as starters or facilitators in the establishment of plants and eventually checking their fate after the ecosystem has been restored. Results revealed that hydroseeding did not prove successful and the vegetation establishment on embankments was mainly from the local seed bank and dispersal from the surrounding area (Bochet et al., 2007b). It concluded that hydroseeding is not needed in the presence of favorable conditions such as suitable climate and slope angle (Matesanz et al., 2005). To improve hydroseeding success on steep slopes efforts need to focus on increasing surface roughness, terracing at regular intervals, or excavating to

produce slope angles below 45 degrees (Bochet & García-Fayos, 2004). Another factor affecting hydroseeding is the slope aspect. Different slope aspects (N, E, S, or W) have various exposures to solar radiation. Bochet et al. (2009) studied the correlation between slope angle thresholds and slope aspect with respect to plant colonization of highly eroded slopes in a semiarid area. They observed that plant colonization started at higher slope angles on north-facing than on south-facing slopes. This difference in the colonization capacity is due to water availability which is controlled by the solar radiation received. Another study in northwestern Spain evaluated the solar radiation effect on short-term herbaceous plant establishment on road cut slopes after hydroseeding. Results showed a significant coincident trend of decrease in plant density, biomass, plant cover, and seedling development along the SE–SW–S gradient (Cano et al., 2002). Additional studies revealed that vegetation establishment was reduced considerably on south-facing slopes due to severe conditions (Andrés et al., 1996; Cano et al., 2002). Aspect influence on early growth dynamics of hydroseeded species in a coal reclamation mine showed that grasses dominated both northern and southern slopes, except during the summer on the southern slope, with grass cover always more on north-facing compared to south-facing slopes (González-Alday et al., 2008). A contradicting study of almost three years involved hydroseeding gypsicolous vegetation on quarry spoil slopes. The two tested slopes (10-15% vs. 60-65%) and two contrasting aspects (north vs. south) revealed that shallow and southern slopes were more suitable compared to northern and steep slopes where non-target species developed readily outcompeting target species (Ballesteros et al., 2017).

A third natural-environmental abiotic factor affecting hydroseeding is the site edaphic characteristic. Soil presence or its absence, erosion, and microclimate are all factors affecting hydroseeding results. Initial soil conditions are the main factor leading to vegetation succession in reclaimed slopes in Mediterranean dry environments (Moreno de las Heras et al., 2008). Preservation of removed topsoil from construction sites is a

valuable resource for ecological restoration. Removed soil contains high concentrations of microorganisms, nutrients (Rivera et al., 2012), native seeds, and organic matter. All are factors that could enhance plant establishment, increasing hydroseeding success rates (Merlin et al., 1999; Agut, 2002.).

With the water running over bare and crusted soils leading to seed removal (Mitchley et al., 1996), the erosion process in Mediterranean climates is an important factor affecting hydroseeding, operating in a catastrophic mode (Wainwright, 1994). A major objective of hydroseeding is to generally control water erosion and the mechanical stabilization of barren slopes (Bochet et al., 2010a). A study in Spain on bare road embankments under construction revealed that the effect of erosion was 30 times more than the vegetated ones (Cerdà, 2007).

As for the microclimate effect, several degraded Mediterranean sites have adverse microclimatic conditions. Such inappropriate microsites, along with water stress, will affect the seedling establishment and plant growth, leading to poor performance of native species in hydroseeding (Tormo et al., 2006). The microclimate established between soil particles and adjacent aggregates will allow partial seed burial enabling a greater chance for successful seedling establishment. The presence of small rocks will also provide shade and shelter, improving the establishment of seedlings (Elmarsdottir et al., 2003).

Water availability is yet another significant natural-environmental abiotic factor affecting hydroseeding success. In a Mediterranean semiarid climate, water availability is a main ecological driver that shapes vegetation (Bochet et al., 2009). Low and irregular distribution of rainfall is a key factor limiting plant growth (Zohary, 1973). Seed arrival to road embankments under Mediterranean climate conditions is not enough to ensure successful plant colonization (Tormo et al., 2006). A study on regolith slopes in southeast Spain concluded that short-lived water availability and high salinity of the regolith seem

to be the key factors limiting vegetation colonization (García-Fayos et al., 2000). Furthermore, recurrent droughts cause not only high rates of plant mortality but also the inability of some species to expand their populations in dry conditions (Cerdà & García-Fayos, 1997, García-Fayos & Cerdà, 1997). Moreover, during the seedling establishment stage, the differences in water availability could explain the very-low plant colonization success and the differential ability of plant species to establish on badland slopes (García-Fayos et al., 2000).

Human-influenced abiotic factors affecting hydroseeding

Human-influenced abiotic factors are factors introduced or modified by direct human interferences aiming to influence hydroseeding outcomes. Described under either direct-hydroseeding practices, varied cultural practices, cost of application, or social factors.

A factor that could directly affect hydroseeding practices is the type of aqueous solution utilized. One study (Merlin et al., 1999) assessed the effectiveness of a group of colloidal substances (of natural and synthetic origin) used in hydroseeding spraying with respect to adhesion, germination, seed growth, and erosion limitations. Results revealed that the desired colloids should have several characteristics: fluidity, adhesion to seeds, enable effective seed germination, be free of material hazardous to the environment, limit erosion, help in restoration or establishment of biological and ecological functions, and is of a low cost.

Alternation of the slurry component is another factor affecting the hydroseeding success. A comparative study (Clemente et al., 2016) using germination tests assessed the effects of different slurry components (bacteria-based fertilizing agent, bio-stimulant, dye, and surfactant) on the performance of a dozen native species used in hydroseeding of quarry slopes. The components affected the germination of 4 out of 12 native species, favoring germination in 2 species (*Thymus mastichia* and *Cistus albibus*)

but delayed it in 2 other species (*Bituminaria bituminosa* and *Helichrysum stoechas*). The study concluded that the effect of slurry components on germination is species-specific; hence any used hydroseeding components should be adjusted to the sown species (Clemente et al., 2016). Another study (Catania et al., 2012) evaluated commercially available seeds on a degraded artificial slope in a southern Mediterranean area for the effectiveness of four different hydroseeding solutions. The study assessed total vegetation cover, hydroseeding vegetation cover, hydroseeding success index, and both the natural and hydroseeded vegetation height. In conclusion, the research revealed that success is conditioned by the type of the mixture components, with mixtures of equal terms earthworm humus and mulch providing the best results in terms of vegetation cover (Catania et al., 2012). The intervention season is another human-influenced abiotic factor affecting hydroseeding. Under semiarid Mediterranean conditions, hydroseeding timing appears to be a critical factor since climatic conditions following hydroseeding significantly affect species' fate. Both climatic conditions and the selection of a suitable species capable of establishing under water-stressed conditions should be considered since both factors are important in determining species performance in sowing (Tormo et al., 2008). If hydroseeding is to be performed out-of-season due to some strict schedule, efforts should focus on improving topsoil and microsite quality rather than increasing seed availability (Mola et al., 2011).

Various implemented cultural practices are other human-influenced abiotic factors affecting hydroseeding. Supplemental irrigation after hydroseeding is one such practice. In a semiarid Mediterranean environment, the application of irrigation after hydroseeding is controversial, with some studies supporting it, whereas other studies highlight a negative role. Studies supporting supplemental irrigation reveal that water stress in a Mediterranean environment highly obstructs plant growth. Therefore, after hydroseeding, irrigation must be applied for a few months due to insufficient rain. This is especially essential since the brief durability of soil water availability largely

determines germination successes (Bochet et al., 2007a; García-Fayos et al., 2000). Another study in Sicily showed that not only mulch and humus are needed, but also irrigation should be carried out during the dry period (Vallone et al., 2013). Other studies recommended the use of drought-tolerant plants along with a careful irrigation plan (Josa et al., 2012). However, other studies raised concerns about irrigation which might lead to the prevention of long-term vegetation establishment due to competition with spontaneous colonizers (García-Palacios et al., 2010). Another study targeting motorway slopes in Spain concluded that fast-growing species dominate the community, rendering irrigation and fertilization of little effect, indicating that hydroseeding neither had a strong impact on vegetation cover nor did it significantly decrease erosion rates of degraded sites in semiarid Mediterranean environments (García-Palacios et al., 2010).

The addition of soil and/or amendments can also be another factor affecting hydroseeding outcomes. Topsoil spreading can improve soil texture, upsurges nutrient soil retention, decreases nutrient loss, reduces sediment runoff, and facilitates quick development of dense vegetation cover (Jimenez et al., 2013). Topsoil addition prior to hydroseeding could be an important technique in roadfill revegetation in Mediterranean environments. This could be achieved by improving soil's physical and chemical properties and also by providing a seed bank to assist spontaneous regeneration (Tormo et al., 2007). A study showed that topsoiling followed by hydroseeding of a selected native seed mixture was the most effective treatment to control erosion on roadfills in terms of cost and benefit (Bochet et al., 2010b). Another study assessing quarry restoration evaluated the contribution of a 30 cm topsoil layer above marble sludge (a material with high water retaining capacity) before hydroseeding. The results indicated an increase in slope water storing capacity, significantly increasing biomass (Simón-Torres et al., 2014). Added topsoil low in organic matter, Fe and Mn, will limit vegetation establishment and development (Bochet & García-Fayos, 2004), therefore,

mixing compost with the soil could improve the germination of native seeds (Hallock et al., 2006).

Mulching is another implemented cultural practice. Mulches and organic amendments can promote seed burial, germination, and establishment, especially if dry soil conditions prevailed (Roberts & Bradshaw, 1985). A study conducted in the Giona Mountain-Greece examined the effectiveness of hydroseeding combined with varied materials. Results showed that hydroseeding alone leads to poor results, but when combined with tilling and mulching, it created satisfactory vegetation cover from the first year after application (Brofas et al., 2007). Mulching could also improve the odds of hydroseeding steep slopes. One study in Cordoba-Spain tested the effectiveness of different mulches (vegetal mulch, humic acids, vegetal mulch with humic acids, and control) on steep slopes. Hydroseeding with the combination of plant mulch and humic acids significantly reduced soil runoff by up to 98.5 percent. This result may be attributed to the combined effect of the protection against raindrop impact and improvement of soil structure brought by organic amendments (Albaladejo et al., 2000). Even in some cases, the total replacement of hydroseeding by spreading a thick compost blanket (pellet form) could enormously benefit seeds germination because of the matting effect, enabling them to withstand harsher and more intensive rainfalls compared to hydroseeding (Tyler, 2003). Gomez et al. (2014) evaluated the effect of three different mats paralleled with hydroseeding for controlling erosion under Mediterranean conditions. The mats used were: Organic mats (made of coconut or esparto grass fiber), synthetic net mats, and synthetic 3D-net mats. Significant erosion control was achieved using different erosion mats combined with hydroseeding, versus control, but showed no clear differences among the diverse matting materials during one year (Gomez et al., 2014).

Cost is yet another factor affecting the decision regarding whether to implement hydroseeding or not. A study compared the cost of different kinds of applications

(broadcasting, drill, and hydroseeding). Results revealed that broadcasting costs ranged from US\$25 to US\$75 /hectare, drilling native seed costs ranged from US\$60 to US\$135 /hectare, and hydroseeding cost was \$1,358 /hectare (Pawelek et al., 2015). A probable reason for the high cost of hydroseeding could be the market price of native seeds. Another study revealed that the prices of selected seed mixtures were 30 times more than that of commercial species, although the cost of relevant ecological advantages provided by the use of native species was only twice that of the commercial species based on cost-effectiveness assessment (Bochet et al., 2010b). Martin et al. (2002) compared the prices (in USD/kg) among different kinds of seeds used for hydroseeding in the semiarid Mediterranean environment. Results revealed a vast range in price range. With prices varying from as low as 2-3.5 USD/ kg for industrially produced species, to 80-120 USD/ Kg for native species (hand-harvested and collected near restoration area), 6-25 USD/ kg for common cultivated wild species, and between 50-850 USD/ kg for the difficult to collect and grow wild species. More demand for native species in restoration projects will probably encourage investing in native seed and plant production, ultimately leading to their abundance at more competitive prices (Bochet et al., 2010b).

Biotic factors affecting hydroseeding

Biotic factors could play a positive or negative role in the outcome of hydroseeding by affecting separately or collectively hydroseeding outcomes (Table 1. 2.). Also, both biotic and abiotic factors might interact, altering the end result.

Human-influenced biotic factors affecting hydroseeding

Through the influence of the soil seed bank, seeds are considered one of the most important actors in the first stages of the restoration process, playing a fundamental role in the composition of future vegetation (Peco et al., 1998). Therefore, the choice of species in seed mixtures is vital when planning a restoration project. Possible guidelines for seed selection could be, the ability of seeds to disperse, produce sufficient viable

seeds, be competitive under local conditions, be of perennial nature, and have a high root/ shoot ratio (Khater et al., 2003). Three groups of seed species are used for hydroseeding: Commercial species, native seed species collected near the intervention area, and native seeds obtained from cultivated wild species (Martin et al., 2002). Commercial species are those plant seed species produced in vast amounts following international norms. Although the use of commercial grasses and legume seeds is probably the most prevalent hydroseeding roadside re-vegetation method (Steinfeld et al., 2007), they frequently give poor results from the very beginning (Andrés & Jorba, 2000; Martínez-Ruiz. et al., 2007). Extremely competitive forage grasses and legumes (ex: *Lolium multiflorum*, *Vicia villosa*, *Festuca arundinacea*, *Medicago sativa*, *Onobrychis sativa*, *Agropyron cristatum*, *Melilotus officinalis*) (Bochet et al., 2010b) are in most locations non-native seeds used for agriculture practices or lawn establishment. Choosing seeds that are not adapted to harsh climatic constraints, like those prevailing in semiarid Mediterranean environments, will lead to failure (Martin et al., 2002), especially with long periods of drought and erosive rains (Bochet & García-Fayos, 2004). A study in west-central Spain evaluated the influence of using commercial seed mixtures in hydroseeding to restore uranium mine wastes under a semiarid Mediterranean climate. Results confirmed the non-suitability of commercial species mixture, suggesting instead the use of local seeds (Martínez-Ruiz et al., 2007). Commercial seed mixtures also give poor results regarding species richness and overall biomass. Since the dominance of certain used species eventually takes over other spreading or native spontaneous ones (Tormo et al., 2008). Therefore, careful assessment of the competitive interactions among commercial and native species is imperative when both seed types are intended for use in a mixture, else it can dramatically affect the outcome of hydroseeding (Matesanz & Valladares, 2007). Using inappropriate species might potentially hinder the establishment of autochthonous species, lead to low diversity in communities, and can even become an integral part of the seed bank causing long-term problems (González-

Alday et al., 2009). The importance of using native species is becoming widely acknowledged, and restoration projects are gradually considering native species for hydroseeding mixtures (Matesanz & Valladares., 2007). Unfortunately, several problems hinder the use of native seeds for hydroseeding in a Mediterranean environment. Concerns such as the scarce availability of information about proper seed collection methods, handling, storage, germination requirements, and seedling culture (Clewell & Rieger, 1997) lead to the narrowing down of choices of seeds used mainly to three main criteria: ecological needs, agro-ecological constraints, and economic feasibility (Khater & Martin, 2007). Odds could be enhanced through species selection, seed pre-treatment, hydroseeding scheduling, and/or manipulation of seeding density and relative species proportion (Oliveira et al., 2012).

Interspecific seed competition is yet another human-influenced biotic factor affecting hydroseeding practices. The kind and percentage of different seeds in a mixture, proportions of native seed densities, varied morphological features, or growth rates are all factors that could affect the end result. Hence, co-seeded species that display more competitive growth traits should be added at a lower proportion (Oliveira et al., 2013). Native species cannot simply be included in re-vegetation 'recipes', since success depends on the density and seedling characteristics of the other co-seeded species. Therefore, their early performances and morphology must be taken into account in the choice of seed mixtures used in restoration actions (Oliveira et al., 2014). Another factor highlighted in literature affecting hydroseeding is the "nurse plant syndrome", defined as the positive influence of adult plants on seedlings (Niering et al., 1963). The harsher the ecological circumstances, the stronger the facilitative effect of nurse plants (Padilla & Pugnaire, 2006). Fast-growing annual species acting as nurse plants may be included with seed mixes of perennial grasses and forbs, providing protection for slower-establishing perennial species by creating shade for a few months after seeds are applied (Skousen & Zipper, 2010). In the semiarid Mediterranean environment, nurse plants will

ultimately decline fast since they can hardly survive such harsh climatic conditions (Zelnik et al., 2010), their residues decomposed by soil microorganisms and nutrients are released back to be used by perennial plant species (Skousen & Zipper, 2010). By rapidly re-establishing vegetation cover, nurse plants can also control erosion, consequently suppressing annual weeds (Mitchley et al., 1996). Zelnik et al. (2010) observed that seed mixtures with nurse species accelerate succession on slopes during the initial years but delay the establishment of late-successional species from the adjacent target vegetation. Hence, recommended that the proportion of nurse species in seed mixtures not exceed 20%.

Mycorrhizal inoculation is another human-influenced biotic factor affecting hydroseeding. Its use, among other inoculants, in restoration actions was recommended for the positive effect on plant establishment, nutrient cycling, ecosystem sustainability (Miller & Jastrow, 1992), improvement of root enhancement (Miller, & Jastrow, 2000), and root branching density- a desirable quality in degraded soils (Stokes et al., 2009). They could also help to stabilize the soil surface and create the assortment needed to increase plant production (Maestre et al., 2011). One of the few studies using inoculum for hydroseeding in a semiarid Mediterranean climate had the objective of selecting an adequate fungus combination (Arbuscular Mycorrhizal Fungi - AMF inoculum), along with legumes and grasses native to the Mediterranean region. The experiment evaluated the implications on severely disturbed areas as well under controlled conditions (greenhouse trial). Results revealed that the establishment of a symbiotic relationship improves aboveground plant growth and increases the legumes/grasses ratio (both in the greenhouse and the field) (Estaun et al., 2007). Another study by Brown et al. (1983) measured rhizobium viability in hydroseeding slurries by testing variations in the pH due to fertilizer addition. They concluded that phosphorus fertilizer as triple-superphosphate significantly reduced the pH leading to the loss of rhizobium viability. The study concluded that phosphorus addition should be in the form of diammonium phosphate

rather than triple superphosphate, ensuring Rhizobial survival, and inoculation of legume seeds (Brown et al., 1983).

Natural-influenced biotic factors affecting hydroseeding

Several perils could impact the fate of the hydroseeded seeds in their intended location, such as weed competition and seed predation. Weed competition was highlighted through a study in a limestone quarry in northeastern Italy evaluating the effect of technical reclamation on the plant community (Boscutti et al., 2017). It concluded that different practices favoring native perennial species (e.g., appropriate seed mixtures, mowing, tree, and shrub planting) could limit weed-control efforts and limit invasive species spread (Boscutti et al., 2017). Another study measuring the basal area of herbaceous Mediterranean species revealed that plants with a large basal area were least suppressed by competition, concluding that a plant's basal area could be used to predict the competitive ability of species performance (Navas & Moreau-Richard, 2005). Seed predation is another natural-influenced biotic factor affecting hydroseeding, through grazing by animals such as birds, mammals, ants (Chambers & MacMahon, 1994), or even pathogens (Hulme, 1998). A study that analyzed different types of seeds actively collected as food items by ants showed that more than 50% of the experimental seeds that were glued to the ground with their own mucilage survived, compared to only 0–20 % of the control seed survival after the same exposure time (Engelbrecht & García-Fayos, 2012).

Whereas most studies in the literature addressed technical issues as barriers to hindering hydroseeding processes, very few articles (Fenianos et al., 2017; 2018) highlighted social factors as issues affecting it. To successfully implement adapted environmental solutions, especially in ecological restoration projects, Fenianos et al. (2017, 2018) investigated possible contributions of cognitive resistance and the need to work on increasing acceptability for adopting new or non-traditional techniques. Using cognitive

flexibility as a mixed approach with awareness-raising sessions positively increased the perception of test groups towards less traditional and more ecological rehabilitation concepts on quarries.

Discussion

Initially developed for ski slopes and side road embankments in northern European countries, hydroseeding as a restoration tool has shown considerable limitations in Mediterranean ecosystems. This review from the semiarid Mediterranean context concludes that the practice of hydroseeding is faced with limited success. A review of the main biotic and abiotic factors as either natural or human-induced that might be affecting it revealed several limiting factors. Some of those factors are site topography and its properties (slope angle, aspect, and microclimate availability), edaphic factors and water availability, cultural practices, the types of seeds used and the interaction among them, and the different perils facing them. Better results can be achieved by incorporating various techniques, such as using nurse plants, ameliorating the soil and its microclimates, supplemental irrigation, the proper choice of seeds, regulating spraying medium, and seed inoculation. Environmental socio-cognitive psychology approaches might help to better convey and increase acceptability towards modified applications of Hydroseeding.

As a consequence, the limits of using hydroseeding as a restoration technique in a semiarid Mediterranean environment call for additional research efforts to sufficiently comprehend its pros and cons.

Supplementary material

Table 1. 1. Primary and secondary keywords used to filter and select the papers used in the methodology.

Primary Search Keywords	Secondary Search Keywords	Author(s)	Title	Year of Publication
Hydroseeding Semiarid Mediterranean environment	History/procedures	Albaladejo Montoro, J. Alvarez Rogel, J. Querejeta, J	Three hydro-seeding revegetation techniques for soil erosion control on anthropic steep slopes.	2000
		Andres, P. Zapater, V. Pamplona, M.	Stabilization of motorway slopes with herbaceous cover, Catalonia, Spain. <i>Restoration Ecology</i> 4:51- 60	1996
		Hölzel, N. Buisson, E. Dutoit, T.	Species introduction—a major topic in vegetation restoration.	2012
		Khater, C.	L'écologie appliquée : une responsabilité scientifique au carrefour de l'interdisciplinarité.	2015
		Matesanz, S. Valladares F. Tena D. Costa-Tenorio M. Bote D.	Early dynamics of plant communities on revegetated motorway slopes from Southern Spain: is hydroseeding always needed?	2006
		Mola, I. Jiménez, MD. López-Jiménez, N. Casado, MA. Balaguer, L.	Roadside reclamation outside the revegetation season: management options under schedule pressure.	2011
		Nunes, A. Oliveira, G. Mexia, T. Valdecantos, A. Zucca, C. Costantini, EA. Abraham, EM. Kyriazopoulos, AP. Salah, A. Prasse, R. Correia, O.	Ecological restoration across the Mediterranean Basin as viewed by practitioners.	2016
		Tormo, J. García-Fayos, P. Bochet, E.	Relative importance of plant traits and ecological filters in road embankment revegetation under semiarid Mediterranean conditions.	2008

		Zdruli, P.	Land resources of the Mediterranean: status, pressures, trends, and impacts on future regional development.	2014
Aftercare measures		Andres, P. Zapater, V. Pamplona, M.	Stabilization of motorway slopes with herbaceous cover, Catalonia, Spain.	1996
		Blondel, J., Aronson, J., Bodiou, J.Y. and Boeuf, G.	The Mediterranean region: biological diversity in space and time.	2010
Nurse plants		Padilla, FM. and Pugnaire, FI.	The role of nurse plants in the restoration of degraded environments.	2006
		Skousen, JG. Zipper, CE.	Reclamation Guidelines for Surface-Mined Land: Revegetation Species and Practices.	2010
		Zelnik, I. Šilc, U. Čarni, A. Košir, P.	Revegetation of motorway slopes using different seed mixtures.	2010
Water		Bochet, E. and García-Fayos, P.	Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia. Spain.	2004
		Bochet, E. García-Fayos, P. Alborch, B. Tormo, J.	Soil water availability effects on seed germination account for species segregation in semiarid roadslopes.	2007a
		Bochet, E. García-Fayos, P. Poesen, J.	Topographic thresholds for plant colonization on semi-arid eroded slopes.	2009
		Bochet, E. García-Fayos, P. Tormo, J.	How can we control erosion of roadslopes in semiarid mediterranean areas? Soil improvement and native plant establishment.	2010a
		Cerdà, A.	Soil water erosion on road embankments in Eastern Spain.	2007
		Cerdà, A. and García-Fayos, P.	The influence of slope angle on sediment, water and seed losses on badland landscapes.	1997

	García-Fayos, P. García-Ventoso, B. Cerdà, A.	Limitations to plant establishment on eroded slopes in Southeastern Spain.	2000
	García-Palacios, P. Soliveres, S. Maestre, FT. Escudero, A. Castillo-Monroy, AP. Valladares, F.	Dominant plant species modulate responses to hydroseeding, irrigation, and fertilization during the restoration of semiarid motorway slopes.	2010
	Josa, R. Jorba, M. Vallejo, VR.	Opencast mine restoration in a Mediterranean semi-arid environment: failure of some common practices.	2012
	Tormo, J. Bochet, E. García-Fayo, P.	Is seed availability enough to ensure colonization success? An experimental study in road embankments.	2006
	Vallone, M. Pipitone, F. Alleri, M. Febo, P. Catania, P.	Hydroseeding Application on Degraded Slopes in the Southern Mediterranean Area (Sicily).	2013
	Wainwright, J.	Anthropogenic factors in the degradation of semiarid regions: a prehistoric case study in Southern France.	1994
Soil addition	Albaladejo Montoro, J. Alvarez Rogel, J. Querejeta, J.	Three hydro-seeding revegetation techniques for soil erosion control on anthropic steep slopes.	2000
	Agut, L.B.	Las limitaciones de la restauración de la cubierta vegetal.	2002
	Bochet, E. and García-Fayos, P.	Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia. Spain.	2004
	Brofas, G. Mantakas, G. Tsagari, K. Stefanakis, M. Varevides, C.	Effectiveness of cellulose, straw and binding materials for mining spoils revegetation by hydro-seeding, in Central Greece.	2007

		Gomez, JA. Rodríguez, A. Viedma, A. Contreras, V. Vanwalleghem, T. Taguas, EV. Giráldez, JV.	Evaluation of different techniques for erosion control on different road cuts in its first year of implantation.	2014
		Hallock, BG. Power, A. Rein, S. Curto, M. Scharff, M.	Analysis of Compost Treatments to Establish Shrubs and Improve Water Quality.	2006
		Jimenez, MD. Ruiz-Capillas, P. Mola, I. Pérez-Corona, E. Casado, MA. Balaguer, L.	Soil development at the roadside: a case study of a novel ecosystem.	2013
		Merlin, G. Di Gioia, L. Goddon, C.	Comparative study of the capacity of germination and adhesion of various hydrocolloids used for revegetalization by hydroseeding.	1999
		Moreno de las Heras, M. Nicolau, JM. Espigares, T.	Vegetation succession in reclaimed coal-mining slopes in a Mediterranean-dry environment.	2008
		Rivera, D. Jáuregui, BM. Peco, B.	The fate of herbaceous seeds during topsoil stockpiling: restoration potential of seed banks.	2012
		Simón-Torres, M. del Moral-Torres, F. de Haro-Lozano, S. Gómez-Mercado, F.	Restoration of dump deposits from quarries in a Mediterranean climate using marble industry waste.	2014
		Tormo, J. Bochet, E. García-Fayos, P.	Roadfill Revegetation in Semiarid Mediterranean Environments. Part II: Topsoiling, Species Selection, and Hydroseeding.	2007
	Microenvironment	Elmarsdottir, A. Aradottir, AL. Trlica, MJ.	Microsite availability and establishment of native species on degraded and reclaimed sites.	2003
		Tormo, J. Bochet, E. García-Fayo, P.	Is seed availability enough to ensure colonization success? An experimental study in road embankments.	2006

Seed type/competition/ inoculation/aqueous solutions	Andres, P. and Jorba, M.	Mitigation strategies in some motorway embankments (Catalonia, Spain).	2000
	Begon, M., Harper, J.L. & Townsend, C.R.	Ecology: From Individuals to Ecosystems.	1996
	Bochet, E. Tormo, J. García-Fayos, P.	Native species for roadslope revegetation: selection, validation, and cost effectiveness.	2010b
	Boscutti, F. Vianello, A. Bozzato, F. Casolo, V.	Vegetation structure, species life span, and exotic status elucidate plant succession in a limestone quarry reclamation.	2016
	Bradshaw, A.D.	The reclamation of derelict land and the ecology of ecosystems.	1987
	Catania, P. Salvia, M. Vallone, M.	Hydroseeding for revegetation in a semiarid Mediterranean environment. In Structures and Environmental Technologies.	2012
	Clemente, AS. Moedas, AR. Oliveira, G. Martins-Loução, MA. Correia, O.	Effect of hydroseeding components on the germination of Mediterranean native plant species.	2016
	Engelbrecht, M. and García-Fayos, P.	Mucilage secretion by seeds doubles the chance to escape removal by ants.	2012
	Estaun, V. Vicente, S. Calvet, C. Camprubi, A. Busquets, M.	Integration of arbuscular mycorrhiza inoculation in hydroseeding technology: effects on plant growth and inter-species competition.	2007
	González-Alday, J. Marrs, RH. Martínez-Ruiz, C.	Soil seed bank formation during early revegetation after hydroseeding in reclaimed coal wastes.	2009
Khater, C. and Martin, A.	Application of restoration ecology principles to the practice of limestone quarry rehabilitation in Lebanon.	2007	

		Khater, C. Martin, A. Maillet, J.	Spontaneous vegetation dynamics and restoration prospects for limestone quarries in Lebanon.	2003
		Maestre, FT. Bowker, MA. Cantón, Y. Castillo-Monroy, AP. Cortina, J. Escolar, C. Escudero, A. Lázaro, R. Martínez, I.	Ecology and functional roles of biological soil crusts in semi-arid ecosystems of Spain.	2011
		Martin, A. Khater, C. Mineau, H. Puech, S.	Rehabilitation ecology by revegetation. Approach and results from two Mediterranean countries.	2002
		Martínez-Ruiz, C. Fernandez-Santos, B. Putwain, PD. Fernández-Gómez, MJ.	Natural and man-induced revegetation on mining wastes: changes in the floristic composition during early succession.	2007
		Matesanz, S. and Valladares, F.	Improving revegetation of gypsum slopes is not a simple matter of adding native species: Insights from a multispecies experiment.	2007
		Merlin, G. Di Gioia, L. Goddon, C.	Comparative study of the capacity of germination and adhesion of various hydrocolloids used for revegetalization by hydroseeding.	1999
		Miller, RM. and Jastrow, DJ.	The application of VA mycorrhizae to ecosystem restoration and reclamation.	1992
		Navas, M. and Moreau-Richard, J.	Can traits predict the competitive response of herbaceous Mediterranean species?	2005
		Oliveira, G. Clemente, A. Nunes, A. Correia, O.	Limitations to recruitment of native species in hydroseeding mixtures.	2013
		Oliveira, G. Clemente, A. Nunes, A. Correia, O.	Suitability and limitations of native species for seed mixtures to re-vegetate degraded areas.	2014

		Oliveira, G. Nunes, A. Clemente, A. Correia, O.	Testing Germination of Species for Hydroseeding Degraded Mediterranean Areas.	2012
		Peco, B. Ortega, M. Levassor, C.	Similarity between seed bank and vegetation in Mediterranean grassland: a predictive model.	1998
		Pywell, R.F., Bullock, J.M., Roy, D.B., Warman, L.I.Z., Walker, K.J. and Rothery, P	Plant traits as predictors of performance in ecological restoration.	2003
		Steinfeld, DE. Riley, SA. Wilkinson, K M. Landis, TD. Riley, LE.	Roadside revegetation: an integrated approach to establishing native plants.	2007
		Tormo, J. García-Fayos, P. Bochet, E.	Relative importance of plant traits and ecological filters in road embankment revegetation under semiarid Mediterranean conditions.	2008
	Slope aspect/steepness	Andres, P. Zapater, V. Pamplona, M.	Stabilization of motorway slopes with herbaceous cover, Catalonia, Spain. Restoration Ecology 4:51- 60	1996
		Ballesteros, M. Cañadas, EM. Marrs, RH. Foronda, A. Martín-Peinado, FJ. Lorite, J.	Restoration of gypsicolous vegetation on quarry slopes: guidance for hydroseeding under contrasting inclination and aspect.	2017
		Bochet, E. and García-Fayos, P.	Factors controlling vegetation establishment and water erosion on motorway slopes in Valencia. Spain.	2004
		Bochet, E. García-Fayos, P. Poesen, J.	Topographic thresholds for plant colonization on semi-arid eroded slopes.	2009
		Bochet, E. García-Fayos, P. Tormo, J.	Road slope revegetation in semiarid Mediterranean environments. Part I: seed dispersal and spontaneous colonization.	2007b
	Cano, A. Navia, R. Amezaga, I. Montalvo, J.	Local topoclimate effect on short-term cutslope reclamation success.	2002	

		Cerdà, A. and García-Fayos, P.	The influence of slope angle on sediment, water and seed losses on badland landscapes.	1997
		Dubayah, R.C.	Modeling a solar radiation topoeclimatology for Rio Grande River Basin.	1994
		García-Fayos, P. and Cerdà, A.	Seed losses by surface wash in degraded Mediterranean environments.	1997
		González-Alday, J. Marrs, RH. Martínez-Ruiz, C.	The influence of aspect on the early growth dynamics of hydroseeded species in coal reclamation areas.	2008
	Socio-economic factors	Bochet, E. Tormo, J. García-Fayos, P.	Native species for roadslope revegetation: selection. validation, and cost effectiveness.	2010b
		Fenianos, J. Khater, C. Viglione, J. Brouillet, D.	Bridging nature and human priorities in ecological rehabilitation projects - a show case from Mediterranean environment - Qattine, Lebanon.	2017
		Martin, A. Khater, C. Mineau, H. Puech, S.	Rehabilitation ecology by revegetation. Approach and results from two Mediterranean countries.	2002

Table 1. 2. Main factors extracted from the literature review that might be affecting the success or failure of the hydroseeding procedure in a semiarid Mediterranean environment.

ABIOTIC FACTORS			BIOTIC FACTORS		OTHER FACTORS
Natural Environmental		Human-Induced	Natural Environmental	Human-Induced	
Site Topography and Properties: <ul style="list-style-type: none"> - Steepness & angle - Aspect 	Direct Hydroseeding Practices: <ul style="list-style-type: none"> - Aqueous Hydroseeding type and properties - Intervention season 	Perils Affecting Seeds: <ul style="list-style-type: none"> - Weed competition - Seed predation 	Seeds Used: <ul style="list-style-type: none"> - Type - Availability & germination difficulties 	Starting Conditions <ul style="list-style-type: none"> - Initial Status of Intervention Area 	
					Soil Physical Characteristics: <ul style="list-style-type: none"> - Soil present/absent - Microenvironment effect
Water Effect: <ul style="list-style-type: none"> - Water availability - Erosion 					

Table 1. 3. Factors affecting hydroseeding result in a semiarid Mediterranean environment (NA - Natural Abiotic factors affecting hydroseeding; HA - Human-induced Abiotic factors affecting hydroseeding; HB - Human-induced Biotic factors affecting hydroseeding)

Variables	Successes	Failures
Slope Steepness	Slight to mild slope steepness - less than 45 degrees (NA) Terracing slopes above 45 degrees (HA)	Unmanaged steep slopes above 45 degrees (NA)
Aspect / Solar radiation	north facing - Low levels of solar radiation (NA)	south facing - High levels of solar radiation (NA)
Soil	Presence of topsoil (conservation of microorganisms, seeds, and nutrients) (NA/HA) Presence of microenvironment: increased soil surface roughness (small rocks, aggregates) (NA/HA) Addition of topsoil or amendments (HA) Mulching (synthetic or organic) (HA) Mycorrhizal soil inoculation (HB)	Absence of topsoil (loss of microorganisms, seeds, and nutrients) (NA/HA)
Water	Water abundancy conditions: regular rainfall (NA) or supplemental irrigation (HA) at germination/seedling phase	Water-stressed conditions: absence / irregular rainfall (NA) or lack of irrigation (HA) at germination/seedling stage
Weeds	Reduction of weed competition through appropriate selection of native seeds mixture (HB)	
Seed choice	Native (NB), competitive ability (NB), colonizing ability (NB), vegetative regeneration ability (NB), market availability (HB), easy to germinate (NB)	Commercial seeds (HB), non-native seeds (HB/NB), seed predation (NB), inappropriate species (HB), lack of native seeds management: collection, handling, storage, etc. (HB)
"Nurse plant" seeds	Recommended for improving hydroseeding successes in harsh ecological circumstances: control erosion, suppress annual weeds, ultimately residues turned into nutrients (HA)	High percentages in seeds mixtures (HA)
Aqueous solution	Adhesive, fluid, free of hazardous material, enabling effective seed germination, limiting erosion (HA)	Might be species-specific (HA)
Cost-effectiveness		High cost per square meter compared to other methods (HA)
Social factors	Increased community awareness and acceptance	Cognitive residence to non-traditional techniques

TRANSITION TO SECOND PAPER

In the preceding section, hydroseeding, an ecological restoration tool, was assessed as a practice in a semiarid Mediterranean environment, reasoning it an unsuccessful technique in several cases. Numerous variables, either of biotic or abiotic nature, hindered its success. Those were further dissected into natural-environmental or human-influenced factors. With several restrictions related to slope aspect and steepness, water problems (high runoff and availability), mixing solutions used, and high implementation costs. Such and other similar surfacing dilemmas materialized a legitimate question: Can ecological restoration in a semiarid Mediterranean environment employ some other appropriate nature-based solutions with fewer problems, have less environmental impact, and is ultimately cheaper? Questions reflecting a vision defined by IUCN as the “Actions to protect, sustainably manage and restore natural or modified ecosystems that address societal challenges effectively and adaptively, simultaneously providing human well-being and biodiversity benefits” (www.IUCN.org). Such methods should be cheaper to apply, have fewer complications, and requires fewer technical skills. One possible nature-based solution is the use of ‘Nurse Plants’ as a tool in ecological restoration. The term ‘Nurse Plant’, coined by Niering et al. (1963), describes plants having positive ‘nursing’ effects on their own or other species under their canopy or in their vicinity (Turner et al., 1966; Steenberg & Lowe, 1969). The impact could be of physical nature (protection from various harsh physical environmental factors like wind, frost, and heat) or biological in nature (protection against predators and herbivores) or even supplying nutrients or moisture.

The next chapter will focus on the potential use of the legume *Trifolium subterraneum* - Fabaceae (Subterranean clover) as a potential nurse plant in supporting newly germinated saplings, initially collected as seeds from the vicinity of an old quarry intended for restoration.

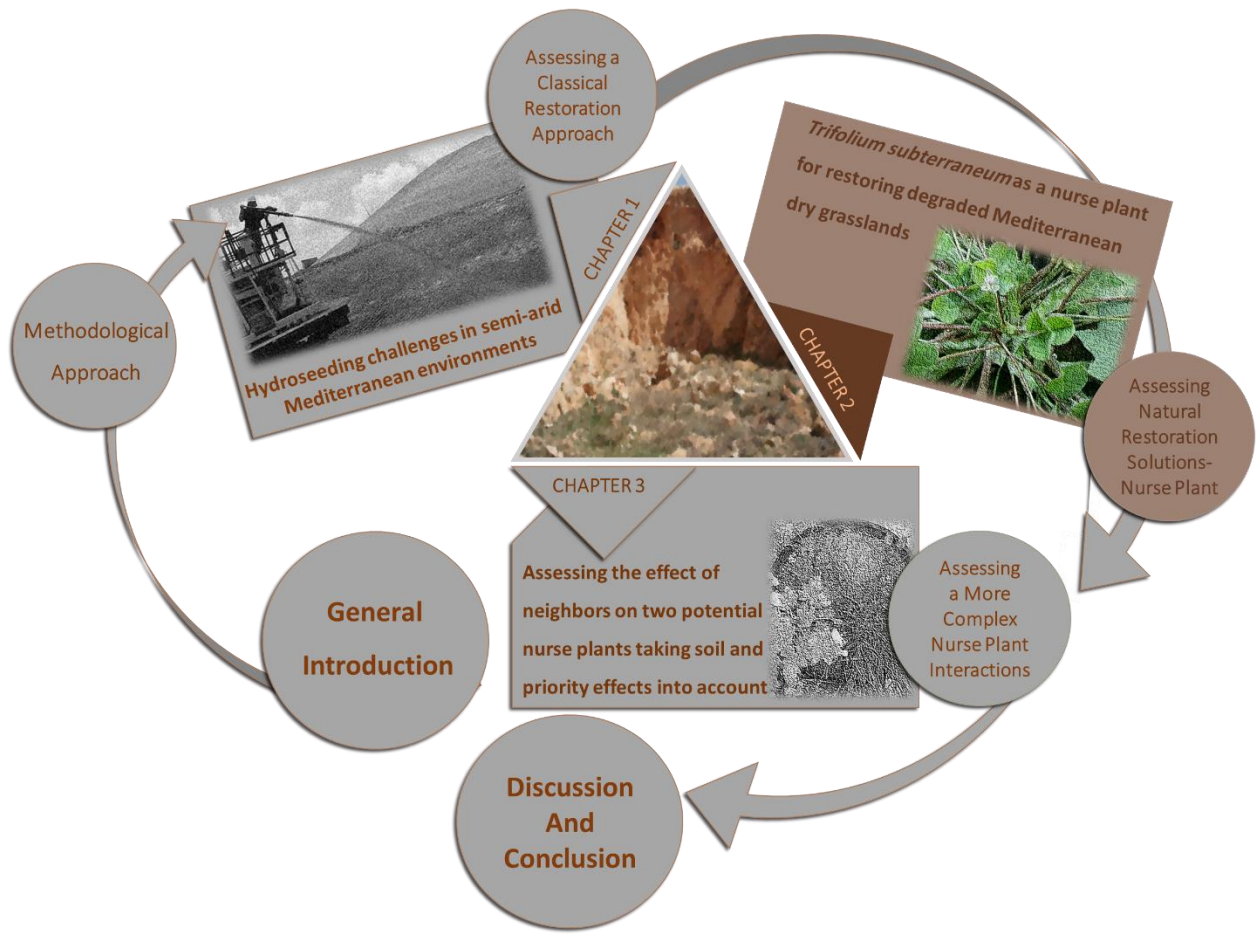


Figure M. 2. Location of chapter two in the general organization of the thesis.

CHAPTER TWO

Is *Trifolium subterraneum* L. a potential nurse plant for restoring soil and degraded Mediterranean grasslands on former quarries in Lebanon?

Results from a 2-year semi-controlled interspecific interaction experiment.

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Abstract

Aim

The radical destruction of Mediterranean herbaceous communities from quarry exploitations leads to changes in species composition, richness, and structure of pre-existing vegetation. In Lebanon, up to 1300 documented quarries destroyed more than 5000 ha of natural and agricultural ecosystems. Such severe degradation necessitates the urgent need for sustainable habitat restoration, preferably through the employment of nature-based solutions. By facilitating the growth and development of other plant species, a nurse plant is a potential natural tool to speed up such regenerative processes. Nevertheless, differences in soil properties and co-existing species may alter plant interactions from facilitation to competition. This study evaluates the interactions of *Trifolium subterraneum* L. (Fabaceae) as a potential nurse species with four co-existing herbaceous plants proposed as target species for restoring a degraded quarry. The experiment utilizes an overgrazed Mediterranean dry grassland surrounding the quarry, identified as the reference ecosystem, for seed and soil supplies, along with utilizing soil collected from the quarry itself, identified as the degraded ecosystem. We evaluated the contribution of the nurse plant towards restoring soil fertility and above-ground plant biomass.

Methods

In a 2-year mesocosm experiment, the interactions between *T. subterraneum* and four co-existing species (*Aegilops triuncialis*, *Echinops viscosus*, *Eryngium creticum*, and *Hyoscyamus aureus*), present in the Mediterranean grasslands of Lebanon, were evaluated. During the first year, *T. subterraneum* (as a potential nurse plant) was grown along with four individuals of each target species in pots filled with soil collected from an abandoned quarry or a nearby dry grassland. The experiment was repeated the second year after mixing the dried *T. subterraneum* biomass into the soil, mimicking the natural incorporation of organic material by trampling ungulates.

Soil analyses were performed from both the reference and degraded soil at the experiment set-up in 2017, after one year of *T. subterraneum* growth before its incorporation in the soil, i.e., without improvement in 2018, and finally after incorporating *T. subterraneum* dry biomass in the

soil, i.e., with soil improvement and the second year of *T. subterraneum* growth in 2019. Indices of Relative Interaction Intensity (RII) were calculated before and after soil improvement on above-ground plant biomass enabling the determination of the plant's competitive ability among the different soil types for the two steps of the experiment.

Important Findings

The soils collected from the reference and degraded ecosystems in 2017 were significantly different in physical and chemical properties. These differences persisted during the second year, despite months of cultivating *T. subterraneum* and target species in pots. After incorporating *T. subterraneum* dry biomass in the soil and growing *T. subterraneum* in the second year, these differences were partially compensated, with a significant increase in dry biomass, C, N, P₂O₅, CEC, and C: N ratio. Still, the improvement of the degraded soil was not enough to reach the levels of the reference soil. Before soil improvement, no soil effect was found in the RII figures with competition dominating the interactions between *T. subterraneum* and target species. Facilitation was only apparent in the biomass of *T. subterraneum* when utilized both as a nurse and target plant in degraded and reference soil. After soil improvement in both soils, a significant outcome was evident in both soil types and among species, with *T. subterraneum* still maintaining a facilitation effect on *T. subterraneum* target biomass only. Likewise, competition remained the dominating interaction with all other target plants, especially in degraded soil.

Conclusion

When cultivated alone as a pure stand (without any other species) and later incorporated as dry biomass into the soil, *T. subterraneum* exhibited facilitative effects on biomass, hence could be recommended as a nature-based solution for increasing soil fertility of degraded quarries. Nevertheless, since *T. subterraneum* showed more competitive interactions than facilitation with co-existing species, we recommend sowing it as a pure mixture the first year, incorporating its dry biomass into the soil to increase fertility, and later seeding target species without reseeding *T. subterraneum*.

Keywords: *Trifolium subterraneum*, nurse plant, facilitation, competition, soil properties, target plants.

Introduction

Assembly rules is an important research topic in plant community ecology that benefits not only in understanding and predicting community trajectories after a disturbance but also aids in determining principal filters that could be manipulated to increase ecosystem restoration success (Palmer et al., 1997; Temperton et al., 2004; Cortina et al., 2006). Interactions between plant species, ranging from competition to neutral uninvolved interactions to facilitation, are significant driving forces in plant community restoration (Brooker et al., 2008). In this context, some plant species are qualified as “nurse plants” and defined as plants that facilitate the growth and development of other plants through positive interaction (Bruno et al., 2003; Padilla & Pugnaire, 2006). Proper selection of a nurse plant can determine the success of a sustainable ecological restoration project since such plants can play an essential role in recovering structures and functions in ecosystems, acting as a driving succession force in some degraded environments (Ren & Liu, 2008).

In severely degraded environments, such as those generated after quarry exploitation, some native plant species could be suitable nurse plants offering microhabitats for target plant recruitment, establishment, and growth (Padilla & Pugnaire, 2006). However, species interactions and the resulting balance between competitive or facilitative interactions depend on disturbances or abiotic constraints (Callaway & Walker, 1997; Olofsson et al., 1999; Laughlin & Abella, 2007; Rajaniemi & Allison, 2009), that develop according to the species involved and the presence of various abiotic filters, such as soil properties or other resources (Callaway et al., 2002; Corcket et al., 2003; Liancourt et al., 2005; Liancourt & Tielbörger, 2009). To assess such processes, mesocosm experiments involving interspecific interactions are appropriate methods, as suggested by Fraser and Keddy (1997) and Hager (2004). However, few works have proposed splitting plant facilitative and/or competitive effects and responses simultaneously. This initial step might enable the identification of potential nurse plants in semi-controlled ex-situ interspecific interaction experiments. Ultimately, utilizing this concept to assist later in restoring soil fertility of degraded areas in-situ.

Although Mediterranean ecosystems represent less than 5% of world terrestrial ecosystems, they exhibit high local biodiversity (Vilà & Sardans, 1999). This study involves the Mediterranean dry

grasslands of Lebanon, which are part of about 4.5 million s.q.m. of land in the Near East region, classified as permanent pastures (Harris, 2000) within the Pre-Steppic Mediterranean Ensemble (MoA/UNEP, 1996). Most of these grasslands are distributed on poor soils in semiarid and arid areas with non-uniformity in the amount and distribution of rainfall and centuries of grazing practices (Darwish & Faour, 2008). Such factors would render ecosystems with low levels of resilience, especially when faced with exogenous perturbations, such as quarry exploitation. In Lebanon, damage from quarry exploitation has grown exponentially due to years of unregulated and chaotic quarrying activities. Between 1996 and 2005, quarries increased by 55.6% (from 711 to 1278 quarries), subsequently increasing quarried land area by 54.4% (from 2875 to 5283 ha). Almost 75 % of these quarries are present in sparse grasslands or bare rocky lands, significantly affecting their sustainable management (Darwish et al., 2011).

This 2-year semi-controlled interspecific interaction experiment aims to comprehend the interactions between a potential native nurse plant (*Trifolium subterraneum*) and itself, as well as four naturally co-existing species (*Aegilops triuncialis* L., *Echinops viscosus* L., *Eryngium creticum* Lam., *Hyoscyamus aureus* L.) all found in the Mediterranean grasslands of Lebanon. It also aims at determining any possible influence of soil physico-chemical characteristics on these interactions. Thus, the effect of two soil types was assessed, the first was taken from an exploited quarry, considered a degraded soil type, and the other was taken from a nearby reference ecosystem and considered a non-degraded soil type. Finally, both soil types were considered for possible improvement by incorporating the dry biomass of *T. subterraneum* grown in pots and repeating the experiment.

Materials and Methods

Study site

The interaction between a potential nurse plant and four target species was evaluated regarding soil properties, in an ex-situ mesocosm experiment performed from 2017 to 2019. Soils were taken from the quarry (degraded soil) and the reference ecosystem (non-degraded soil), an overgrazed Mediterranean dry grassland surrounding the quarry.

The experiment took place in an ex-situ setting due to the following reasons: (1) The possibility to have precise and better control when assessing interspecific-relationship amongst the same group of plants comprising four target plants (of the same species) against one specific potential nurse plant with controlled environment factors (pot volume, soil moisture, soil fertility, and soil granulometry). (2) The facility of applying the intended procedure considering that the work has been conducted on five different plant species. (3) The presence of several overpowering external variables at in-situ location associated with uncontrolled grazing, unrestricted pedestrian traffic, complexity and roughness of the working site, and the difficulty in getting clearance to access the location classified as a security-zone area.

Potential nurse plant

***Trifolium subterraneum* L.**



Figure 2. 1. *Trifolium subterraneum* tested as a potential nurse plant. (Shaiban, IMBE).

***Trifolium subterraneum* as a potential nurse plant in restoration**

Nurse plants are potential restoration tools in disturbed lands (Zhao et al., 2007; Gómez-Aparicio, 2009) and extreme environments, with native species being one of the most appropriate choices as nurse plants intended to improve environmental circumstances for sapling establishment

(Padilla & Pugnaire, 2006), enhancing soil moisture, organic material, and trap seeds offering physical shelters (Bertness & Callaway, 1994). In arid (Arriaga et al., 1993), and semiarid regions, almost a third of nurse plants are leguminous plants capable of fixing nitrogen through a symbiotic relationship with root-nodulating bacteria (Flores & Jurado, 2003), leading to an enhancement in soil nitrogen availability (Barnes & Archer, 1996), hence, an improvement in soil nutrient content (den Hollander & Bastiaans, 2007). This characteristic is very important in Mediterranean soils, where nitrogen is a chronically scarce nutrient (Alpert & Mooney, 1996), leguminous species can be good candidates as potential nurse species for Mediterranean soil and herbaceous plant community restoration.

T. subterraneum has been considered a theoretical foundation species capable of restoring nitrogen-depleted fields, with a crucial role in community structuring, regulating plant diversities, or modifying ecosystem development (Bruno et al., 2003; Ellison et al., 2005). *T. subterraneum* (Figure 2. 1.) is native to the Mediterranean Basin, west Asia, and the Atlantic coast of western Europe (Zohary & Heller, 1984; San Miguel, 1994), growing on dry soils of open plains and mountains, ranging from sea level up to an altitude of 1800 m (Ecocrop, 2017), also native to Lebanon (one of 49 *Trifolium* sp. found naturally in Lebanon) (Tohmé & Tohmé, 2014). The species, part of the Fabaceae family (Zohary & Heller, 1984), is a multi-stemmed therophytic species (Raunkiaer, 1934), flowering from March-April, and setting fruits in April-May (Vasileva et al., 2016). Several calyces of the upper-most sterile flowers form a drilling apparatus allowing formed heads to penetrate the soil (geocarpy) (Falistocco et al., 1987), transforming into a buried pod. *T. subterraneum* has high ecological flexibility, with its habitats ranging from sparse oak forests to pastures. Because of its soil covering properties and nitrification attributes (Vasileva et al., 2016), It is considered a versatile plant used for weed suppression (Due to size & low spread), green manure (producing 112 to 224 kg N/ha), mulching substance (dry mulch in late spring & green mulch in fall), grazing (being very palatable), nitrogen fixing (Clark, 2007), and erosion control (Howieson et al., 2000). Other desirable qualities include an annual life cycle coinciding with abundant rainfall (from autumn to spring), tolerance of regular and close grazing (due to prostrate growth habit), and natural regeneration and seed burying (reducing the need for re-seeding), consequently, protecting its seeds from being eaten by stock (Nichols et al., 1994). As a legume species, *T. subterraneum* is a nitrogen-fixing plant (Ferreira & Castro, 2005) co-existing

with vesicular-arbuscular mycorrhizas (VAM) or with *Rhizobium leguminosarum* biovar *trifolii* bacteria species, allowing it to fix about 50 to 188 kg/ha of nitrogen per year (Sanford et al., 1994; Bolger et al., 1995). Coiffait-Gombault et al. (2012), experimenting in the Crau semiarid steppe in southern France, revealed an improvement in soil nitrogen content two years after sowing *T. subterraneum*, leading to an increase in the productivity of other foundation species such as *Brachypodium retusum* and *Thymus vulgaris*. As a feed source, *T. subterraneum* is considered worldwide as the greatest contributor amongst all annual clovers to livestock feed production and soil improvement (McGuire, 1985; Kirilov & Vasileva, 2016). As a nurse plant, *T. subterraneum* has been selected previously for restoring soil fertility and regeneration of some Mediterranean dry grassland species. Results revealed improvement in the survival and growth of target species in Mediterranean semiarid ecosystems due to increased soil nitrogen content (Padilla & Pugnaire, 2006). In southern France, *T. subterraneum* sown directly into a semiarid natural plant community resulted in a forage quality improvement, a significant increase in plant productivity, and a gain in sheep weight gain (Molénat et al., 1998). *T. subterraneum* is also considered a classic example of how a species from one world region has proved to be of immense value when introduced to other regions (Frame & Laidlaw, 2005). In Australia alone (where it was introduced), *T. subterraneum* is considered the most widely seeded annual pasture legume species, with over eight million hectares sown in Western Australia and an estimated 29 million hectares seeded in Southern Australia (Hill & Donald, 1998).

Target species for restoration

The experiment aims to provide evidence of positive interactions, under contrasted soil characteristics, between the legume species *T. subterraneum* and itself and also on four target species: *Aegilops triuncialis* L., *Echinops viscosus* L., *Eryngium creticum* Lam., and *Hyoscyamus aureus* L. (Figure 2. 2.), chosen for the experiment because of: (1) Abundance in the reference ecosystem (and in Lebanon's dry Mediterranean grasslands). (2) Suitability as target plants for restoring Mediterranean grasslands in Lebanon following any degradation (such as quarry exploitation). (3) Their seeds exhibit high germination rates under a controlled environment.



a. *Aegilops triuncialis*



b. *Echinops viscosus*



c. *Eryngium creticum*



d. *Hyoscyamus aureus*

Figure 2. 2. The various target species used in the study, all are abundant in the Mediterranean grasslands of Lebanon (Shaiban, IMBE- Google images- Google images- Shaiban, IMBE).

***Aegilops triuncialis* L.**

The genus *Aegilops* L. belongs to the tribe Triticeae, within the Pooideae subfamily, in the Poaceae family. *Aegilops triuncialis* (Figure 2. 2a) (Common English name: barb goatgrass- Common Arabic name: دوسر طويل - *dawsar taweel*), a cleistogamous with a selfing rate estimated at 97% (Pajkovic et al., 2014), is the most widely distributed species within the genus (Maxted et al., 2008), spreading throughout southern Europe, the Mediterranean Basin, and Asia. The species is generally abundant in dry and partially disturbed habitats, dry-rocky slopes, edges of and within cultivated fields, matorrals, grasslands, shrubs, woodlands, and open forests. It is also found in steppes up to desert margins, river terraces, and even at the seaside, predominantly growing on limestone and basalt. The species grows on various soil textures, but mainly on clay and sandy loam. It grows under a wide range of annual rainfall, ranging from 125 mm to 1,400 mm, from sea level to 2,700 m (van Slageren, 1994).

***Echinops viscosus* L.**

The genus *Echinops* L. (Asteraceae, Cardueae) contains around 120 species distributed all over the world, particularly in the Northern Hemisphere (Garnatje et al., 2004a), with most species number occurring in the Caucasus and the Middle East (Jäger, 1987). It is predominantly a perennial genus, with very few annual species (Garnatje et al., 2004b). The species *Echinops viscosus* - synonyms including *E. spinosissimus* subsp. *macrolepis* (Boiss.) Greuter, *E. viscosus* subsp. *macrolepis* (Boiss.) Feinbrun, *E. viscosus* DC. var. *macrolepis* Boiss., *E. syriacus* Boiss - Common English name: Viscous globe thistle. Common Arabic name: شوك الجمل - *Shawk el-Jamal*). It is characterized by uni-flowered capitula aggregated into second-order spherical or oval heads, this syncephalia being a unique feature within the tribe (Petit, 1997). *E. viscosus* is a spiny perennial forb, 80-100 cm tall flowering May-August (Figure 2. 2b). In Lebanon, it is present in numerous locations, such as dry and rocky slopes, scrublands, roadsides, fields, grasslands, and abandoned lands in sunny stretches (Arnold et al., 2015).

***Eryngium creticum* Lam.**

The genus *Eryngium*, which comprises about 250 species in the family Apiaceae, is considered the largest and arguably the most taxonomically complex in its family and is distributed in the temperate regions of every continent (Calvino et al., 2008). The genus is distinguished from other

Apiaceae members by a capitate inflorescence and the presence of a single bract per flower (Calvino et al., 2008). The species *Eryngium creticum* Lam. (Common English name: Field Eryngo – Common Arabic name: قرص عنة- *Kors Anne*) is a spiny perennial, sometimes a biennial or an annual, glaucous and glabrous herb, reaching up to 50 cm in height with an erect and branched stem. The stem leaves are sessile and palmately divided into 3–8 prickly lobes, flowering from May to August (Kikowska et al., 2016) (Figure 2. 2c). Its habitat is dry or damp sites, growing in several soil types, on hillsides, cultivated or abandoned lands, and cliff crevices (Arnold et al., 2015). Found in the eastern Mediterranean region at low altitudes in sunny locations, frequently in Lebanon, Palestine, Jordan, and Syria (Kikowska et al., 2016).

***Hyoscyamus aureus* L.**

The *Hyoscyamus* genus is medicinally important within the nightshade family, Solanaceae. A small herbaceous genus of 20 species occupying Europe, northern to north-eastern Africa, and the phytogeographical Sino-Japanese region, (Nasir, 1985). *Hyoscyamus aureus* (Common English name: Golden Henbane- Common Arabic name: بنج زهبي- *Banj zehabee*) is a glandular-villous perennial species with a golden yellow corolla and purple throat, found in several eastern Mediterranean countries such as Turkey, Cyprus, Iraq, Syria, Lebanon, Israel, Jordan, and Egypt (Brandes, 2002) (Figure 2. 2d). Along with pollens of other species, *H. aureus* pollen was also identified in the famed Shroud of Turin, and the plant still grows on the old citadel walls of Jerusalem (Frei, 1983).

Experimental design

Soil and seed collection

Soil collection

Soil samples needed for the experiment were extracted from a quarry (degraded site) located in the vicinity of the small village of Maqneh (34.0787° N, 36.2095° E) in the eastern Beqaa plain-Lebanon (Figure 2. 3.). This quarry is part of the Cenomanian-Turonian Rock Formation (C4-5), composed of dolomitic limestone with a few dolomite inclusions (Figure 2. 4.). The reference soil samples were extracted from the nearby Mediterranean dry grassland (reference ecosystem) (Figure 2. 5.). A total soil volume of 14m³ (from both reference ecosystem and degraded quarry)

was collected from the top 10 cm layer and transported by truck (Figure 2. 6.) to the intended experimental site located in the small village of Zahrieh (33.884790° N, 35.706560° E), in Mount Lebanon- Lebanon.



Figure 2. 3. General location of the quarry site where the soil was extracted- Maqneh, Beqaa plain, Lebanon. (Modified from Ecomed, 2016).



Figure 2. 4. Quarry, the degraded ecosystem. (Shaiban, IMBE)



Figure 2. 5. Reference overgrazed old grassland ecosystem in formerly cultivated terraces located next to the quarry. (Shaiban, IMBE).



Figure 2. 6. Transporting collected soil from the quarry and nearby reference ecosystem to the experimental site. (Shaiban, IMBE).

Seed collection

The local flora in the reference ecosystem surrounding the quarry is very diverse and is of botanical importance due to the presence of rare and endemic species (*Campanula euclasta*, *Stachys niveaa*, *Alcea damascena*, and *Astragalus roussaeanus*) and steppe species (*Serratula cerinthifolia*, *Convolvulus dorycnium* ssp. *oxysepalus*, *Capparis spinosa* ssp. *parviflora*, *Parietaria judaica*, *Alkanna orientalis*, and *Moluccella laevis*), as well as frequent and abundant species (like those selected for the experiment). This richness in diversity combined with plant endemism ultimately renders restoration of the intended quarry in Maqneh of importance. The seeds of the four-target species (*A. triuncialis*, *E. viscosus*, *Er. creticum*, and *H. aureus*) were all hand-harvested towards the end of the flowering season from the vicinity of the quarry in a radius of 0.5 Km (September - 2017). All collected seeds were air-dried in the shade for one month, threshed, cleaned, and placed in tightly closed plastic boxes with ball-shaped fumigant insecticide, Naphthalene (C₁₀H₈) added to eliminate any possible existing larvae or adult

insects (Romano, 1966). The seeds of *T. subterraneum* were obtained from Fertiprado Company (France) since the needed quantity for the experiment was not sufficient. In parallel, seed samples (100 seeds of the five species) were tested for germination in Petri dishes at the Institute of Mediterranean Biology and Ecology (IMBE) laboratory in Avignon, France. All the seeds were placed in a growth chamber (temperature 15/20°C, 08/16h - night/day) and watered regularly. Coleoptile emergence, used as a proxy of germination, was recorded every 2-3 days for eight weeks. The results obtained from the laboratory, with more than 60% germination rate, ensured reliable germination of all seeds needed for the intended research (Table 2. 1.).

Mesocosm experimental site

The research took place in a tunnel-greenhouse dedicated to this experiment (Figure 2. 7.) (a south-facing, closed structure sheathed with a 200-micron plastic sheet) reclined at an altitude of 700 m.a.s.l. in the small village of Zahrieh (33.8920° N, 35.6758° E)- Mount Lebanon- Lebanon.



Figure 2. 7. The general setting of the site location of the experiment, along with the tunnel greenhouse. Zahrieh village, Mount-Lebanon, Lebanon. (Shaiban, IMBE).

Design and procedure

Although the experiment is a whole continuous study, it could be divided into three phases, spanning from 2017 to 2019.

These phases encompass:

- A preparation phase (2017), where required seeds and soils were collected (for testing and analysis at set-up time and for the experimental set-up in the greenhouse). The soil result analysis performed at this phase will be referred to in the manuscript as "at set-up time".
- An experiment to evaluate the effect of *T. subterraneum* on target species on both the degraded and the reference soils without soil improvement (2018). The measurements and analyses performed on these data will be referred to in the manuscript as "without improvement".
- An experiment to evaluate the effect of *T. subterraneum* on target species on both the degraded and the reference soils after soil improvement. To achieve this *T. subterraneum* was grown independently for one year in pots of both degraded and reference soils. Once dead, its dry biomass was incorporated into both soil types before running a one-year experiment evaluating the effect of *T. subterraneum* on target species (2019). The measurements and analyses performed on these data will be referred to in the manuscript as "with improvement".

Soil preparation and analyses

The soil used in the experiment was immediately sieved through a 2-mm sieve mesh, mixed with perlite (an inert material used to ventilate, loosen, and increase soil drainage) at a ratio of 10:1, and filled in 22.5 cm diameter pots (5-liter pots). A 3 cm layer of pebbles (size 0.5-1 cm), was placed at the bottom of each pot before adding soil for drainage. A 2mm-thick geotextile fabric separated the bottom pebble layer from the soil, preventing soil loss and permitting appropriate water drainage.

To test soil at set-up time, ten soil samples, each weighing 100g, were randomly selected from both sites (five from each the reference and degraded ecosystem), dried and sieved through a 2-mm mesh sieve, and were tested for various physical (Table 2. 2.) and chemical properties (Table 2. 3.) at Teyssier Laboratory (Bordeaux - France). Soil analyses were also run on degraded soils from the pots without soil improvement after one year of *T. subterraneum* grown with its targets, and on degraded soils from pots with soil improvement, after one year of *T. subterraneum* being

grown alone and incorporated into the soil and the second year of *T. subterraneum* grown with its targets. The performed soil analysis covered the following parameters: pH water ratio 1:5 (Thomas, 1996), CaCO₃ using a Bernard Calcimeter (Sparks et al., 1996), organic C (Allison, 1965), Total N by dry combustion (Bremner, 1996; Dumas, 1831), C: N ratio, Cation Exchange Capacity (CEC), exchangeable K⁺ (Metson et al., 1956; Ciesielski et al., 1997), plant-available P (Olsen et al., 1954), and the particle-size distribution in 5 fractions without prior decarbonization (clay- less than 0.002 mm, fine silt- between 0.002-0.02 mm, coarse silt- between 0.2-2 mm, fine sand- between 0.05-0.2 mm, and coarse sand- between 0.2-2 mm) (Robinson & Friedman, 2003).

Performed experiments

At the initiation of the experiment, all seeds were germinated in plastic trays to avoid any initial failures during the early seedling growth phase and to reduce weed competition in the pots from the soil seed bank of the original soil (Figure 2. 8.). The germination took place within a germination chamber at a 22/24 °C, 08/16h - night/day, using a germination medium that consisted of a 2:1 ratio mixture (two parts soil from either reference or degraded ecosystem to one-part regular seed-germination medium). Once the seedlings developed beyond the cotyledon phase into the first set of true leaves, they were all transferred to the designated greenhouse. In the greenhouse, seedlings were placed under a 50% shade net for three days, allowing them to harden and acclimatize to fluctuating day and night temperatures, and to gradually adapt to direct sunlight under greenhouse conditions. Finally, they were all transplanted into intended pots.



Figure 2. 8. Seed germination in trays. (Shaiban, IMBE).

In total, 220 pots were divided equally into 110 pots filled with soil from the reference ecosystem and 110 pots from the degraded ecosystem. All the pots (110 pots of both soil types), were further separated into 55 pots for the first-year experiment and 55 pots for the second-year experiment (Figure 2. 9.).

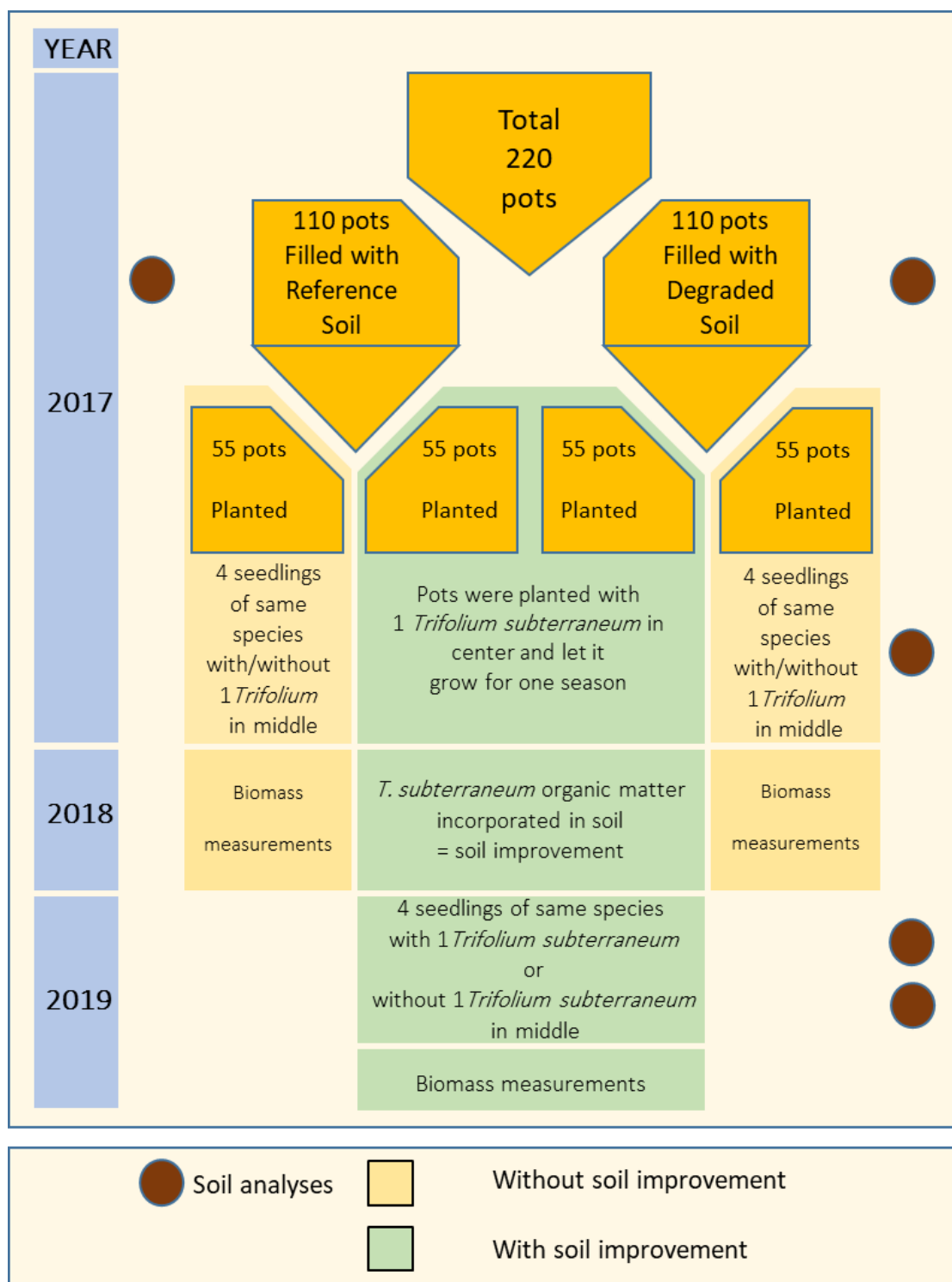


Figure 2. 9. Schematic representation of the procedure for the 3 years experiment.

Pots, spaced at inter / intra-row distance of 20 cm, were placed on a concrete floor to eliminate any emerging voluntary weeds. A drip-irrigation system, with individual online drippers, was assigned to each pot (adjustable 0 to 40 lit/ hr. - Rain Bird Corporation, attached by a 2mm

spaghetti tube rising from a 16mm polyethylene irrigation pipe- Elysee Irrigation Ltd). Throughout the experiment, water purposed for irrigation was pumped up from an artesian well and stored in a 1000-liter plastic tank, allowing any undesirable particles to precipitate before irrigation. Initially, after soil filling but before planting, all pots were thoroughly watered for two weeks enabling any germinated voluntary weeds to be pinched out with minimal soil disturbance. Moreover, throughout the experiment, all weed seedlings that germinated were regularly uprooted.

The experiment followed the competition protocol suggested by Gaudet and Keddy (1988, 1995), with four seedlings of the same species transplanted equidistantly in each pot, plus one *T. subterraneum* seedling planted in the middle, as the potential nurse plant (5 plants in total) (Illustration 2. 1b). In another group (Illustration 2. 1c), *T. subterraneum* was omitted. In yet a third group (Illustration 2. 1a), the potential nurse plant *T. subterraneum* was planted alone in the middle. Finally, in the last group of pots, the potential nurse plant *T. subterraneum* planted in the middle along, with four seedlings of *T. subterraneum* transplanted equidistantly (Illustration 2. 1d). All pots were watered only when the soil surface dried out at a depth of about 1 cm. All of the above treatments were replicated five times.

The second group of pots (110 pots) was filled equally with soil from the reference and degraded ecosystems and were all planted with *only one* seedling of *T. subterraneum* in the middle (Figure 2. 9.) and left to grow for its whole lifecycle (seedlings stage, vegetative growth and spreading, inflorescences, seed set, and finally dying). After seven months, the dried *T. subterraneum* plant material was harvested, chopped into 2-3 cm fragments, re-incorporated in the soil, and kept aside (five months-period) until the next growing season. At the beginning of the following growing season, the exact procedure implemented during the first season was precisely re-applied to those set-aside pots repeating all planting combinations and replicating five times.

During the experiment, minor pest attacks were observed, with snails being the most obvious. Miniature snails hid beneath the rim of the pots during the day to munch on the foliage at night. A bi-weekly inspection under pot rims was sufficient to put the problem under control. It is worth noting that after transplanting, a few of the initially planted *T. subterraneum* (about 5%) did not develop, flourish, or establish properly. This issue could be due to the failure to establish a

symbiotic relationship with any Mycorrhizal fungi (Chambers et al., 1980; van der Heijden & Sanders, 2003).

Plant measurements

Performance of both *T. subterraneum* and target species was assessed in early summer, corresponding to the phenological stage of fructification of the target species, and prior to completion of the life cycle of annual species in late summer. The functional trait measured was the total above-ground biomass of the vegetative parts (Gaudet & Keddy, 1988; Rösch et al., 1997; Navas & Moreau-Richard, 2005). Measuring the above-ground biomass of all plants necessitated cutting their vegetative parts at the soil level, storing them in separate coded paper bags, and oven-drying at 50°C for 48 hours. Finally, all bagged plant samples were weighed (digital balance with a precision of ± 0.01 grams). Despite measuring the biomass, surface area, and height of all plants, the only data considered to be the precise and reliable trait is the biomass, eliminating some unreliable disparities and inaccuracies (for example, some shade that might affect total height or any crowding of mature plants from adjacent pots affecting the surface area....).

Data collected from the interaction between *T. subterraneum* and target plants was assessed by applying the Relative Interaction Intensity Index (RII) to plant biomass. RII was the tool chosen to evaluate the interaction because of the following mathematical and statistical properties: (1) It is symmetrical in relation to zero, with identical absolute values for competition and facilitation (from -1 to 0 indicates competition and from 0 to +1 indicates facilitation), (2) It is linear, and (3) It has no discontinuity within its range (Howard & Goldberg, 2001; Armas et al., 2004; Liancourt et al., 2009).

RIIs were calculated according to the following equation:

$$RII_{\text{effect}} = \frac{(\text{Biomass}_{N\text{withTrifolium}} - \text{Biomass}_{N\text{withoutTrifolium}})}{(\text{Biomass}_{N\text{withTrifolium}} + \text{Biomass}_{N\text{withoutTrifolium}})}$$

Where biomass is measured on N= the average biomass of four targets of one species (*A. triuncialis*, *E. viscosus*, *Er. creticum*, *H. aureus*, or *T. subterraneum*), biomass was measured in the

presence or absence of the potential nurse plant *T. subterraneum*. As there were four individuals of each target species/pot, their average biomass was considered.

Statistical analyses

Soil statistical analyses

All analyses were performed with R-3.6.0 (R Core Team 2020). Prior to applying statistical analysis to soil physico-chemical variables, all data distributions were examined using the Shapiro–Wilk test of normality. GLMs with Gaussian distribution were calculated to investigate the effects on soil physico-chemical variables when data were normally distributed. GLMs with gamma distribution were applied for data that violated the assumption of a normal distribution. Models were followed by Tukey HSD post-hoc tests using the `glht` function with $P < 0.05$ from the "multcomp" package (Hothorn et al., 2016).

Plant statistical analyses

To assess the competitive effect of *T. subterraneum* (ability to reduce the performance of target species), two-way ANOVAs or two-way ART ANOVAs (Aligned Ranks Transformation ANOVAs) were performed on the RII_{effect} respectively, without soil improvement and with soil improvement. The interaction of two explanatory variables was tested for (1) the type of soil (reference vs. degraded) and (2) the identity of the target species. ANOVAs were applied when data responded to the hypotheses of normality and homogeneity of variance. ART ANOVAs were performed when otherwise (Mangiafico, 2016). All were followed by pairwise contrast comparisons with a Tukey adjustment when significant. In order to find out if each RII was significant from zero, thus indicating competition or facilitation, a Wilcoxon test was performed on each level of explanatory variables.

To study the effect of *T. subterraneum* as a nurse plant a GLM test was performed on target species biomass grown only on degraded soils. The interaction of two explanatory variables was tested (1) in the presence of *T. subterraneum* as a nurse plant and (2) whether degraded soil was improved or not. All models were fitted with a Gamma error distribution followed by pairwise contrast comparisons with a Tukey adjustment when significant.

Results

To make things more comprehensible during the flow of this document the following terms will be used: Any test results from both degraded and reference soils at the initiation of the experiment will be referred to as *at the time of set-up* ("*set-up*" in figures captions), whereas results after planting but prior to incorporating dried biomass into soils as *without soil improvement* ("*w/o imprv*" in figures captions) and finally results after incorporating dried biomass into soils as *with soil improvement* ("*w imprv*" in figures captions).

Soil results

Degraded soil at the time of set-up vs. Reference soil at the time of set-up.

In 2017, before initiating the experiment, soil samples extracted from the degraded quarry and nearby reference site were tested. The obtained results revealed significant differences in both physical and chemical properties between the collected samples from the degraded ecosystem (abandoned quarry) and nearby reference ecosystem (surrounding grassland).

Soil physical properties

Soil collected from the degraded ecosystem was significantly higher in clay ($251.2 \pm 14.6b$ g/kg) compared to the reference ecosystem ($209.6 \pm 9.8a$ g/kg). Furthermore, in the degraded soil, both fine and coarse sand results were significantly lower when compared to reference soil. Fine sand in degraded soil was $101.0 \pm 5.2b$ g/kg soil vs. $145.0 \pm 5.5a$ g/kg reference soil, and coarse sand was $143.2 \pm 17.4b$ g/kg in degraded soil vs. $203.8 \pm 7.7a$ g/kg in reference soil. Whereas in both degraded and reference soils, fine and coarse silt were not significantly different (Table 2. 2.).

Soil chemical properties

The significantly higher clay value in degraded soil correlated to significantly higher CEC in degraded soil ($14.7 \pm 0.5a$ meq/ 100g soil) at the time of set-up vs. reference soil ($12.16 \pm 0.2b$ meq/ 100g soil) at time of set-up. Degraded soil also showed a significantly higher water-pH in degraded ($8.6 \pm 0.03a$) than in the reference ($8.4 \pm 0.02d$). Also, a significant difference in pH-KCL between degraded ($7.8 \pm 0.02a$) and reference ($7.74 \pm 0.02b$) was observed (Table 2. 3.). A significant difference was also present between the Total dry biomass, which was significantly

lower in the degraded soil ($0.8 \pm 0.02b$ meq/100g soil) than in the reference soil ($1.63 \pm 0.03b$ meq/100g soil) (Figure 2. 10.). Total nitrogen in degraded ($560 \pm 4a$ mg/kg soil) was also significantly lower than in the reference soil ($1068.2 \pm 27.7d$ mg/kg soil) (Figure 2. 11.). The measured carbon content was also significantly lower in degraded soil ($4.6 \pm 0.1b$ mg/kg soil) than in the reference soil ($9.5 \pm 0.2b$ mg/kg soil) (Figure 2. 12.). Significant differences were also found for phosphorus, being significantly lower in degraded soil ($34.8 \pm 0.4a$ mg/Kg soil) than in the reference soil ($58.6 \pm 0.4d$ mg/Kg soil) (Figure 2. 13.). Total Ca, K, CaO, and C:N ratio were all not significantly different between soil types (Table 2. 3.).

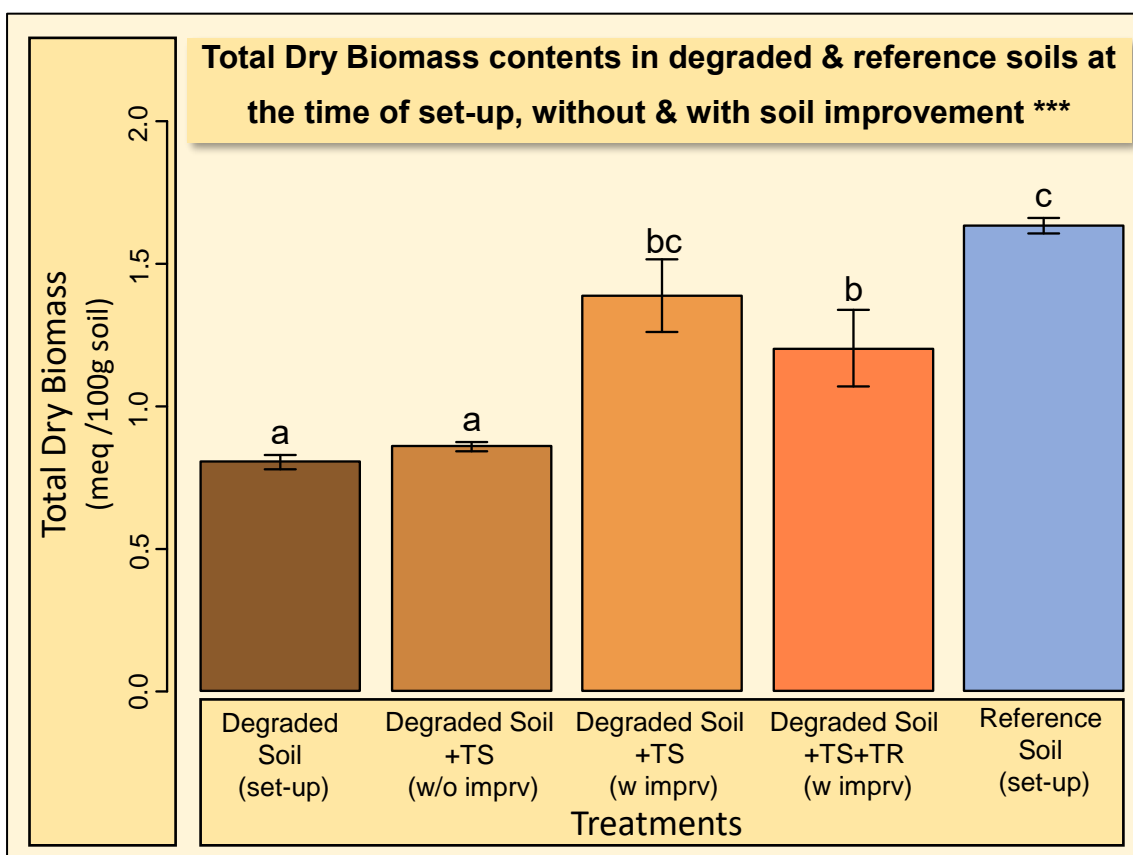


Figure 2. 10. Dry Biomass contents measured in-situ degraded soils and reference soils at set-up, with the different treatments applied in the pots to the degraded soil at the time of set-up, without soil improvement, and later with soil improvement ($F=20.5$, $P<0.001$). TS is *Trifolium subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.

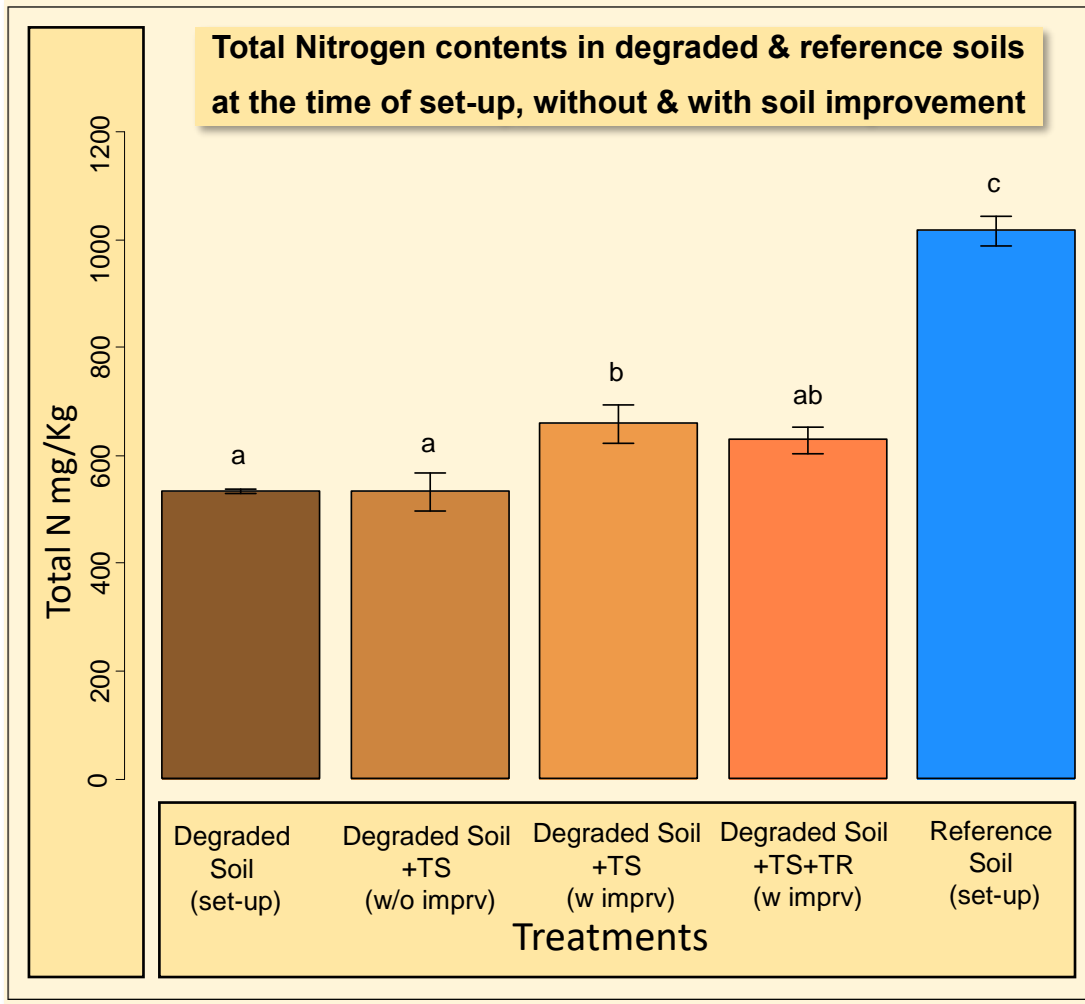


Figure 2. 11. Total Nitrogen contents measured in-situ degraded soil at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement ($F= 52.5$, $P<0.001$). TS is *Trifolium subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.

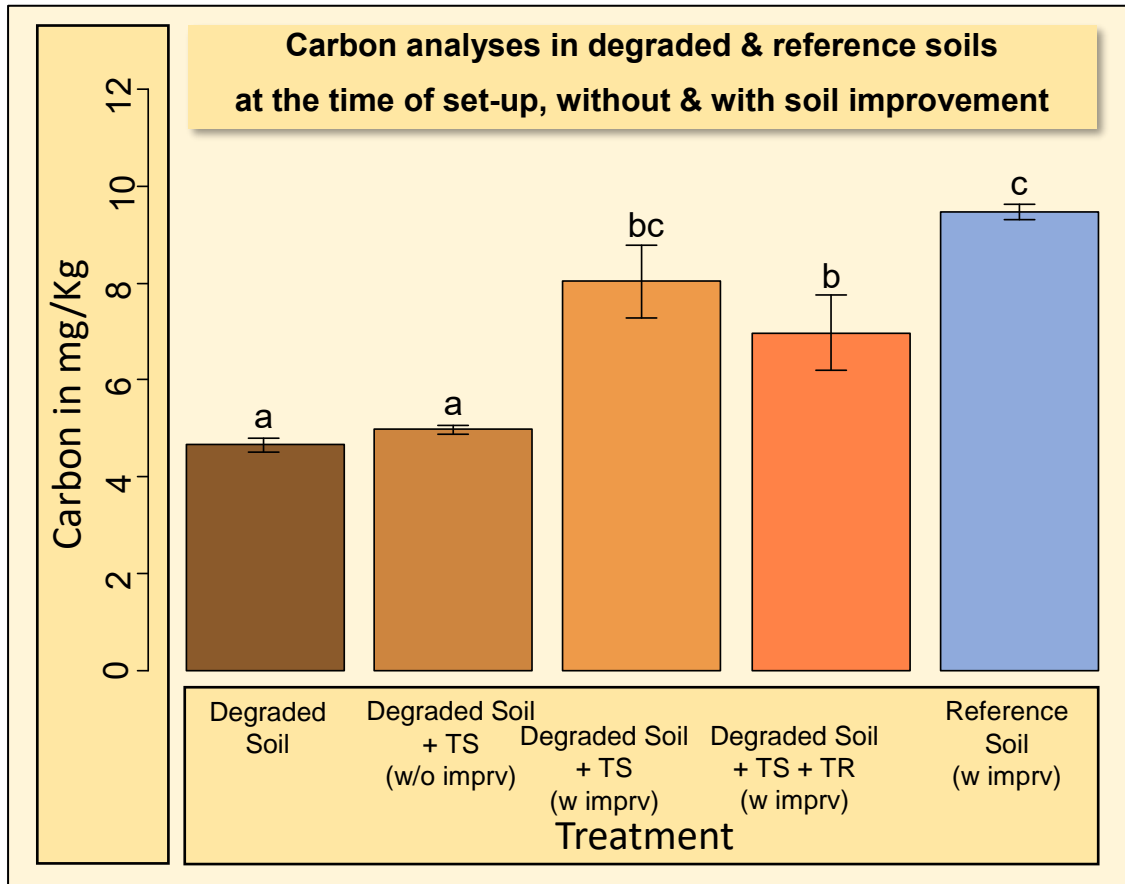


Figure 2. 12. Soil Carbon analyses performed for in-situ degraded soil and reference soil at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement ($F= 20.5, P<0.001$). TS is *Trifolium subterraneum*- TR is Target plants- “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement.

Degraded soil at set-up time vs. degraded soil without improvement

Although *T. subterraneum* and target species were grown for several months, there were few significant differences in soils after these species were grown without improvement when compared to the initial figures of degraded soil at set-up time. There was a significant increase in available phosphorus levels (34.8 ± 0.4 mg/kg vs. 42.8 ± 1.4 mg/kg respectively) (Figure 2. 13.). Also, CaO and NaO increased significantly between the degraded soil at set-up time and in degraded soil without improvement (21.8 ± 0.4 mg/kg vs. 90.4 ± 14.4 mg/kg respectively). Another noteworthy figure was a significant reduction in potassium when comparing its levels between the degraded soil at set-up

time and in degraded soil without improvement (300.2 mg/kg vs. 192.2 mg/kg respectively) (Figure 2. 14.).

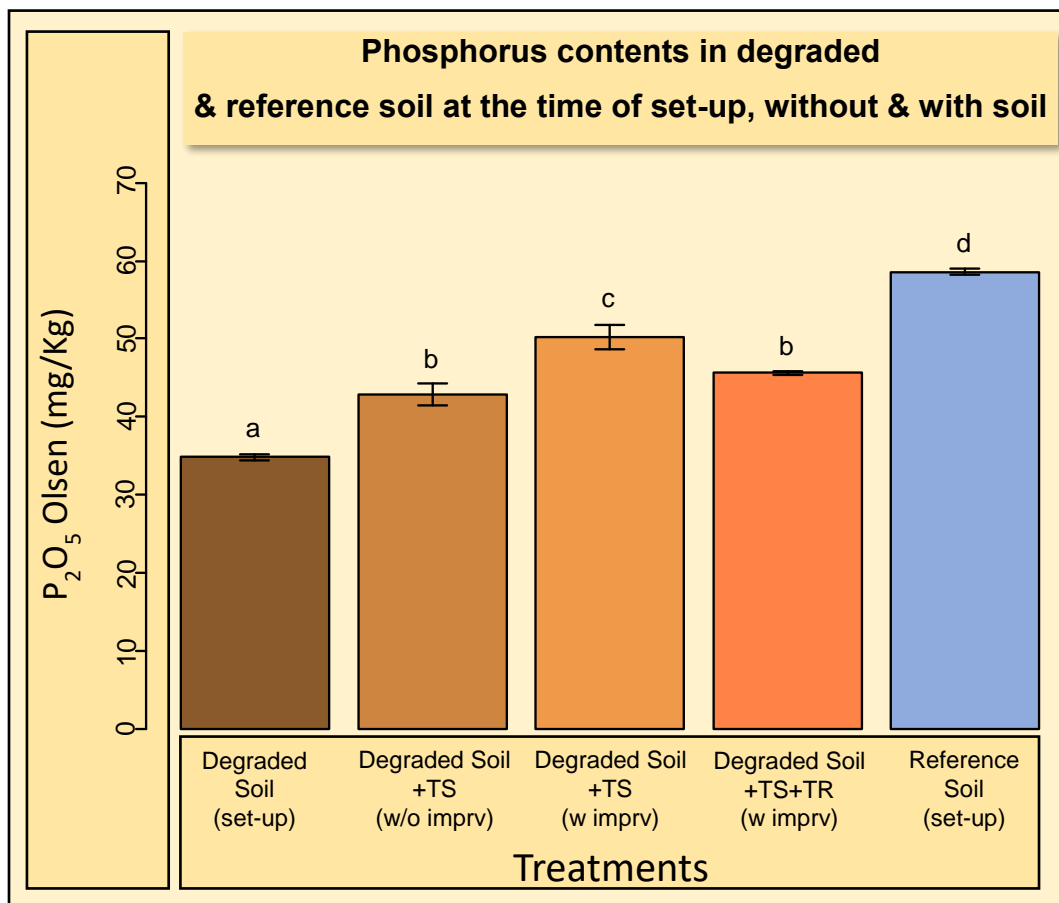


Figure 2. 13. Available Phosphorus contents measured in-situ degraded soil and reference soil at the time of set-up and with the different treatments applied in the pots to the degraded soil without soil improvement and with soil improvement (F= 83.9, P<0.001). TS is *Trifolium subterraneum*- TR is Target plants- "set-up" is at the time of set-up- "w/o imprv" is without soil improvement- "w imprv" is with soil improvement.

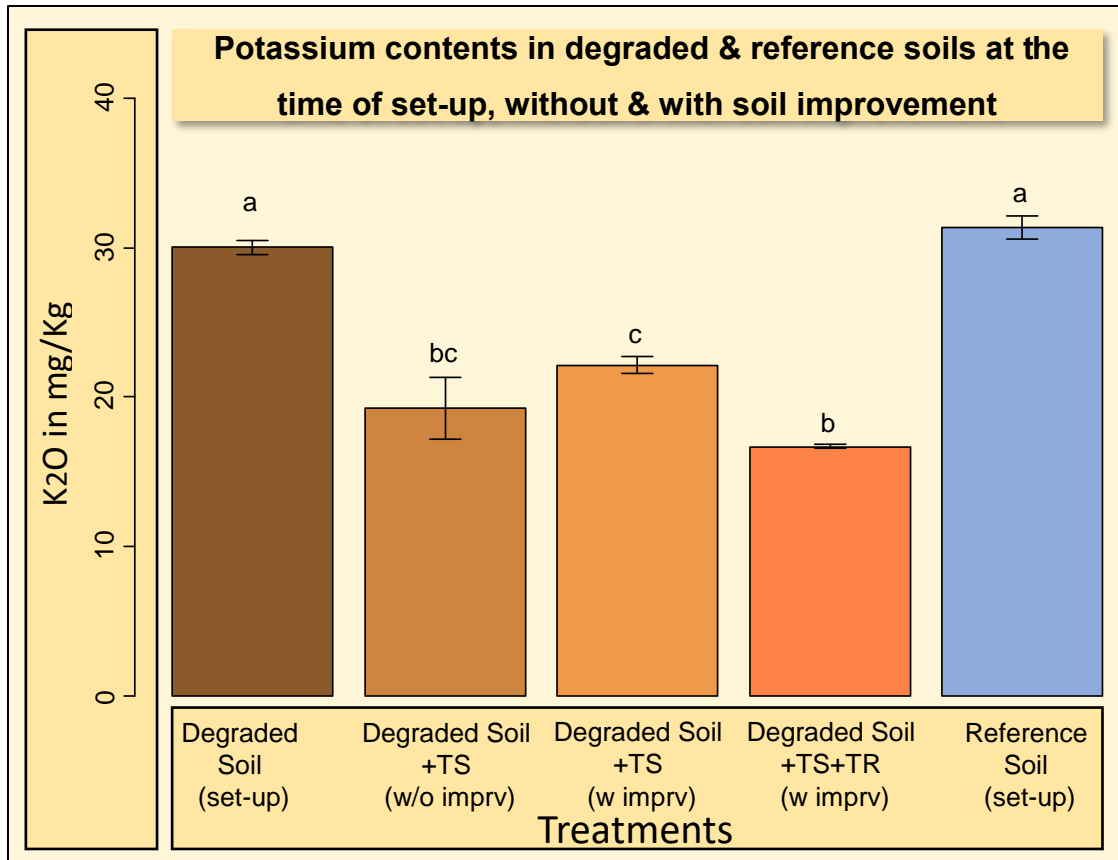


Figure 2. 14. Potassium contents measured in-situ degraded soil and reference soil at the time of set-up, and the different treatments applied in the pots to the degraded soil without soil improvement and later after soil improvement ($F= 28.3, P<0.001$). TS is *Trifolium subterraneum*- TR is Target plants. - "set-up" is at the time of set-up- "w/o imprv" is without soil improvement- "w imprv" is with soil improvement.

Degraded soil at set-up time vs. degraded soil after improvement

A significant decrease in CEC (Table 2. 3.) was noticeable in improved soils compared with the degraded soil at set-up time ($11.5 \pm 0.4b$ meq/ 100gr and $14.7 \pm 0.5a$ meq/ 100g, respectively). Although no significant increase in dried biomass was present between soil at set-up time and degraded soil without improvement, significant changes appeared following soil improvement, reflected as an increment from 0.8 ± 0.02 meq/100g in degraded soil at set-up time up to 1.39 ± 0.1 meq/100g soil in degraded soil after improvement, with *T. subterraneum* growing alone, and a bit less but still significant with *T. subterraneum* growing with target plants (1.2 ± 0.1 meq/100g soil) (Figure 2. 10.). Carbon also increased significantly with soil improvement (Figure 2. 12.). However, it is worth noting that after improvement both Total dried biomass and C amounts were still below those in the reference soil (OM in reference soil 1.63 ± 0.03 meq/100g soil, C in

the reference soil 9.5 ± 0.2 mg/Kg) (Figure 2. 10. & Figure 2. 12.). Total soil nitrogen was significantly higher in degraded soil with improvement than in degraded soil at set-up time when *T. subterraneum* was grown alone (692 ± 36.9 mg/kg vs. 560 ± 4 mg/kg respectively), and marginally significant when *T. subterraneum* and target plants were grown together (659.4 ± 26.4 mg/kg soil). Still, it is worth noting that the nitrogen level was significantly higher in the reference soil (1068.2 ± 27.7 mg/kg) (Figure 2. 11.).

Phosphorus significantly increased between degraded soil at set-up time ($34.8 \pm 0.4a$ mg/kg) and all degraded soils with a treatment (soil without improvement: $42.8 \pm 1.4a$ mg/kg; soil with improvement and on which *T. subterraneum* was grown alone: $50.2 \pm 1.5c$ mg/kg; soil with improvement and on which *T. subterraneum* + target plants were grown: $45.6 \pm 0.2b$ mg/kg). Nevertheless, it is worth mentioning that the phosphorus level on degraded soils did not attain the phosphorus level of the reference soil ($58.6 \pm 0.4d$ mg/kg soil) (Figure 2. 13.).

A common concern that appeared in both the degraded soil without improvement and with soil improvement, as opposed to the time of set-up, is an increase in sodium contents (Table 2. 3.). The test results showed a spike in sodium level in degraded (at the time of set-up: 21.8 mg/kg soil against 90.4 mg/kg soil without soil improvement & 231.6 mg/kg soil with soil improvement).

Effect of both Trifolium subterraneum and soil improvement

There was no significant positive effect of the improvement of degraded soil on target biomass (i.e., biomass after soil improvement was not significantly higher than before soil improvement). On the other hand, *A. triuncialis* and *H. aureus* had higher biomass without soil improvement, and *E. viscosus* had higher biomass without soil improvement when grown with *T. subterraneum*. Furthermore, *T. subterraneum* reduced the biomass of *Er. creticum* but increased that of *T. subterraneum* grown as target plants, confirming $R_{I\text{effect}}$ results below (Figure 2. 15.).

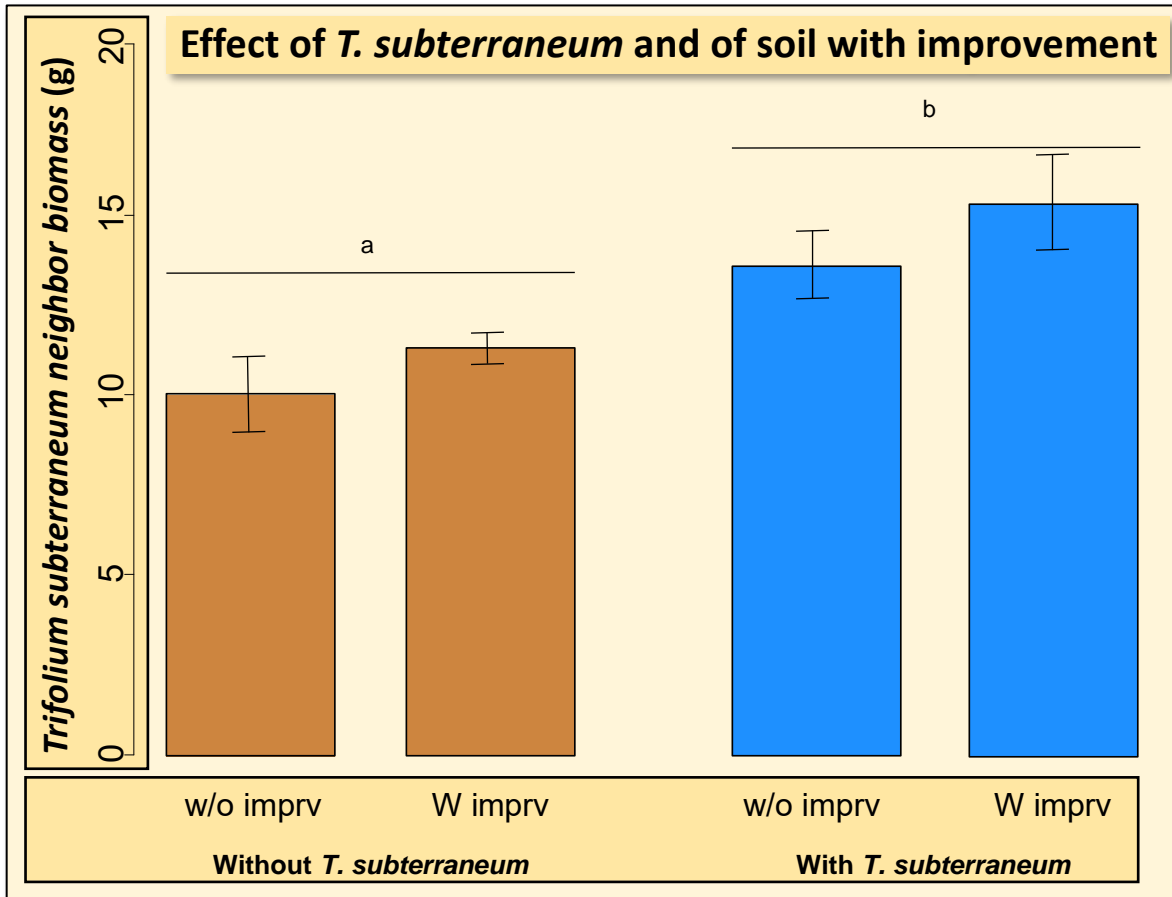


Figure 2. 15. Effect of *Trifolium subterraneum* as a nurse plant, and soil improvement on target *T. subterraneum* biomass grown on degraded soils ($\chi^2=0.30$, $p<0.001$, $n = 5$). Bars sharing a letter were not significantly different from each other ($p<0.05$). “set-up” is at the time of set-up- “w/o imprv” is without soil improvement- “w imprv” is with soil improvement. Without *T. subterraneum* = Without *T. subterraneum* as a nurse plant; With *T. subterraneum* = With *T. subterraneum* as a nurse plant

RII results

Effect of *Trifolium subterraneum* on target plant biomass (RII_{effect})

No significant soil effect was apparent on the RII indices without soil improvement on target. Alternately competition dominated the interactions between *T. subterraneum* and the four-target species in both soil types (reference and degraded). This effect was slightly competitive to neutral on three target species but only significant on *Eryngium* sp. Noticeably, *T. subterraneum* as a potential nurse plant had a significant facilitative effect on *T. subterraneum* targets, reflected through greater biomass as a target plant when grown with *T. subterraneum* in the center of the pot ($F=2.89$, $p=0.034^*$; Figure 2. 16.).

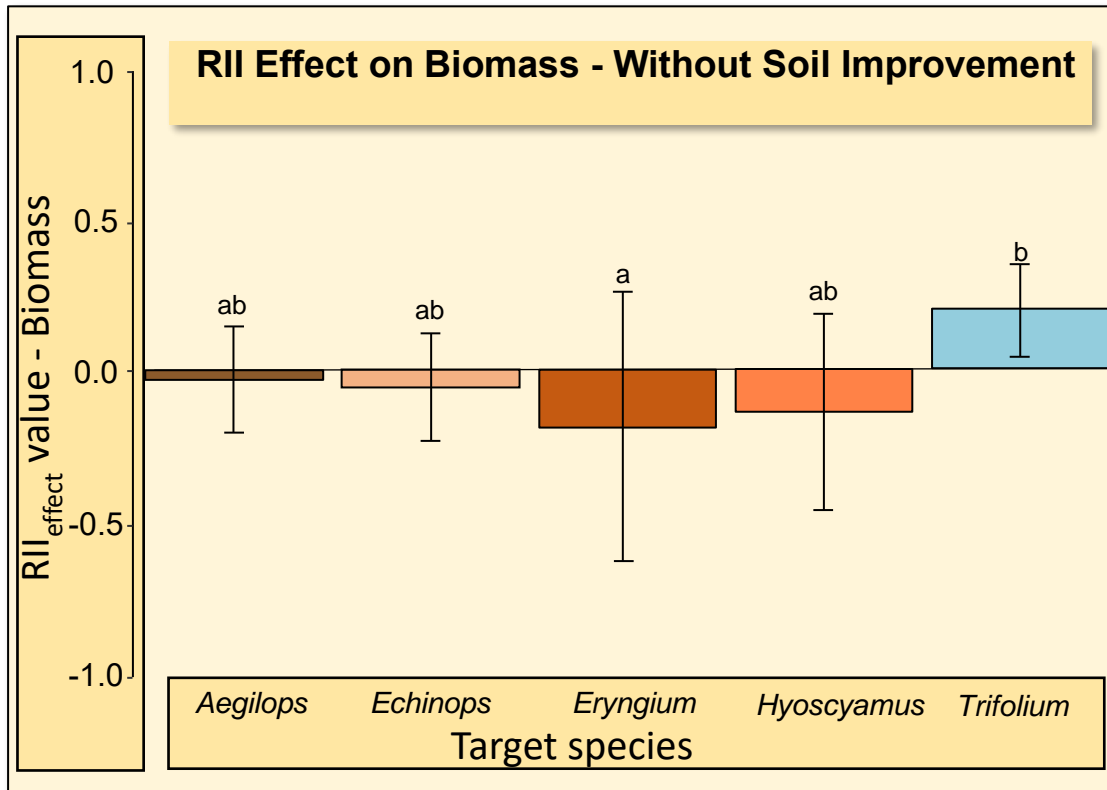


Figure 2. 16. Effect of *Trifolium subterraneum* on neighbor species biomass depending on neighbor species identity without soil improvement ($F=2.89$, $p=0.034^*$): mean RII effect per replicate pot ($n = 5$). The horizontal line marks $RII = 0$, above which positive RII values indicate facilitation and below which negative values indicate competition. Species sharing a letter were not significantly different from each other ($p < 0.05$). Box-plots colored light blue show RII significantly different from 0 (tested by Wilcoxon test).

Nevertheless, after soil improvement in both reference and degraded soils, a few significant results appeared. However, the most important was the persistence of facilitation of *T. subterraneum* on *T. subterraneum* target biomass, whatever the soil type ($F=12.65$, $p < 0.001^{***}$; Figure 2. 17.). The competitive effect of *T. subterraneum* was significant on degraded soil ($F=8.30$, $p=0.006^{**}$, $V = 60$, Figure 2. 18.).

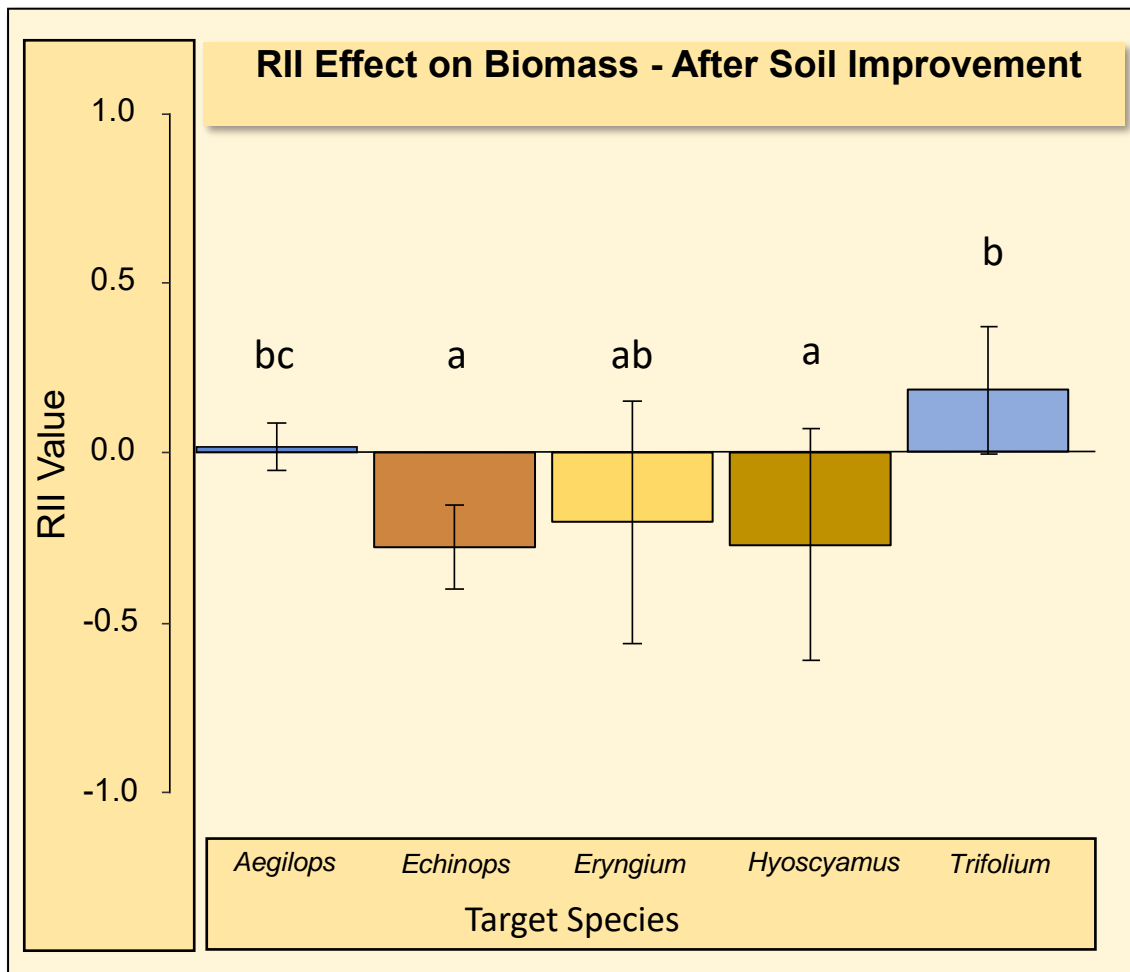


Figure 2. 17. Effect of *Trifolium subterraneum* on target species biomass depending on target species identity after soil improvement ($F=12.65$, $p<0.001^{***}$). Mean RII effect per replicate pot ($n = 5$). The horizontal line marks $RII = 0$, above which the positive RII values indicate facilitation and below which the negative RII values indicate competition. Species sharing a letter were not significantly different from each other ($p<0.05$). Box-plots colored light blue show RII significantly different from 0 (Tested by Wilcoxon test).

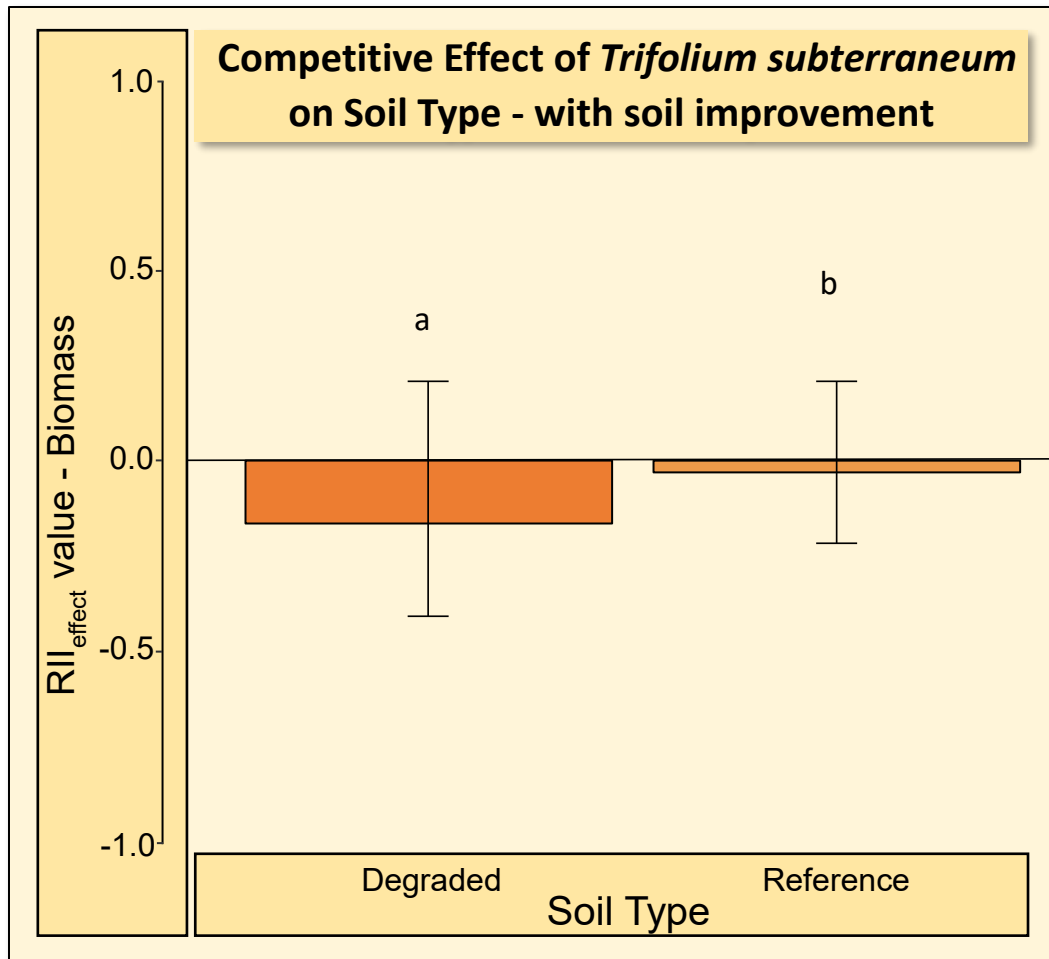


Figure 2. 18. Effect of *T. subterraneum* on target species biomass depending on soil type after soil improvement ($F=8.30$, $p=0.006^{**}$). Mean RII effect per replicate pot ($n = 5$). The horizontal line marks $RII = 0$, above which positive RII values indicate facilitation and below which negative values indicate competition. Soil types sharing a different letter were significantly different from each other ($p<0.05$). Box-plots colored light blue show RII significantly different from 0 (tested by Wilcoxon test)

Discussion

Soil results

Before initiating the experiment, soils tested from the reference and degraded ecosystems revealed significant differences in some physical and chemical properties caused by the impact of the quarry exploitation on the soil's upper layers (removal by extraction or erosion in the

slopes surrounding the quarry). Degraded soil had a significantly higher clay proportion than reference soil, leading to a significantly higher CEC. Also, the degraded soil had significantly higher pH (water-pH and pH-KCL), contrary to a lower pH that would generally lead to a reduction in CEC as in the case of reference soil. After soil improvement, the soil analyses showed a significant decrease in CEC compared to the degraded soil at set-up time. This decrease might be due to cations absorption by the growing plants, with no possible replacement, specifically since the experiment was conducted in pots without any fertilizer addition.

At the initiation of the experiment, dried biomass was significantly lower in the degraded soil when compared to the reference soil with its higher availability of vegetation cover. There was also no significant change in dried biomass quantity between degraded soil at set-up time and afterward, prior to soil improvement phase. Eventually, the dried biomass significantly increased after the soil improvement phase with *T. subterraneum* grown alone or with target plants (though a bit less), leading to a significant increase in total carbon and total nitrogen at post-soil improvement vs. at the time of set-up. Adversely, from a restoration perspective, and even after soil improvement through incorporating *T. subterraneum* into the degraded soil, total OM, carbon, and nitrogen levels- although improved- remained lower than the levels of OM, carbon, and nitrogen in the reference soil. Therefore, to restore the biomass to a level significantly close to that of reference soil, and since solely depending on cultivating *T. subterraneum* and incorporating it in soil was not sufficient, an additional source of biomass must be considered. Accordingly, the grazing and trampling of flocks in quarries intended for restoration could be regarded to encourage microbial growth and activity, ultimately increasing both soil fertility and quality (Garris et al., 2016; Luna et al., 2016).

Significant differences were also evident in phosphorous concentration between the reference and degraded soil collected from the quarry, with an elevated amount in the latter. This difference might be present since phosphorus does not readily leach out of the root zone and is potentially lost only by erosion and runoff. A significant increase in available phosphorus was shown later in the soil without improvement, possibly due to the degradation of total phosphorus into available phosphorus from the soil minerals under root actions and the emission of weak acids (Noack et al., 2012; Vet et al., 2014). An increase in dried biomass is also a relevant factor

in controlling phosphorus availability, since the addition of dried biomass (via dry material incorporation) leads to organic phosphorus mineralization through the exudation of organic acids or phosphatase enzymes by plant roots or mycorrhiza (Jones & Darrah, 1994). This mineralization of dried biomass provides a significant portion of the phosphorus needed for the plants (California Fertilizer Association, 1995). A significant increase in phosphorous was also evident within the degraded soils at set-up time and with soil improvement, in *T. subterraneum* alone and with *T. subterraneum* and target plants. Still, it is worth highlighting that the phosphorus level in degraded soil did not attain the phosphorus level in reference soil.

A significant reduction was also noted in potassium levels when comparing the amount in degraded soil collected at set-up time, without soil improvement, and after soil improvement. This issue may be due to the high tendency of *T. subterraneum* to absorb potassium from the soil (Rossiter, 1955; Barrow, 1966), a fact that is amplified further in pots, where the lost potassium is not compensated easily in the same manner observed in nature.

Also, the sodium level increased significantly between both soils taken at set-up time (degraded and reference) and soil with or without improvement. In abundance, sodium can degrade soil structure, slow infiltration rates, and interfere with Ca, Mg, and K uptake (Hodges, 2010). This increase in sodium level could be a bias attributed to salt accumulations which gradually increase in the irrigation water after being pumped from the artesian well. This bias was diminished considerably during the progression of the experiment due to the initial storing of the water pulled from the artesian well in a separate tank, leaving it to settle before using it for irrigation and utilizing new hoses.

RII results

Gaudet and Keddy (1988) revealed that measurements (such as total aboveground biomass, surface area, etc.) are prime indicators of either facilitation or competition amongst tested species. The results in this experiment confirmed that *T. subterraneum* had a competitive effect- which in some situations is a major driving factor structuring plant communities (Kimball et al., 2013)- rather than a facilitative effect on the four tested target plants (Rösch et al., 1997; Howard & Goldberg, 2001; Navas & Moreau-Richard, 2005). The obtained results revealed a significant

reduction in total aboveground biomass for almost all target species in both the reference and degraded soil, whether improved or not.

Previous studies in the literature highlighted nurse plants as facilitators under harsh environmental conditions (Franco & Nobel, 1988; Bertness & Hacker, 1994; Tielbörger & Kadmon, 2000; Cavieres et al., 2002; Verdú & García-Fayos, 2003), with almost a third of such plants in arid (Arriaga et al., 1993) and semiarid regions being leguminous (Flores & Jurado, 2003). Notably, *T. subterraneum* enhances nitrogen content in the soil, improving the survival and growth of target species (Padilla & Pugnaire, 2006, Coiffait-Gombault et al., 2012). The contrary was apparent in this study, with results aligned with previous studies in Mediterranean ecosystems (e.g., Vilà & Sardans, 1999; Liancourt et al., 2009; Prévosto et al., 2012), where competition, not facilitation, was the dominating outcome of plant interactions, with or without improvement in soil fertility resulting from the incorporation of *T. subterraneum* dried biomass into the soils. Nevertheless, results clearly show that in the degraded soils, even at low nutrient levels (particularly for N, P₂O₅, C, and OM), *T. subterraneum* - like almost all nitrogen-fixing plants- flourished utilizing efficiently available elements (especially N). This aspect is reflected through better vegetative growth, more biomass accumulation, and size increase when compared to the target plants with no nitrogen-fixing capabilities, gradually weakening the target plants via competition. When cultivated as a pure stand, *T. subterraneum* exhibited facilitation effects on biomass, ultimately incorporated as dry dried biomass into the soil for improvement.

Consequently, from a restoration perspective, *T. subterraneum* could be endorsed as a species assisting in soil fertility re-establishment in a degraded quarry. Nevertheless, it should be introduced independently during the first growing season as a pure stand foundation species (Coiffait-Gombault et al., 2012)- since facilitation was evident between *T. subterraneum* as a nurse plant and *T. subterraneum* as a target plant. With its ground-hugging nature, *T. subterraneum* will spread on the soil surface, restraining ruderal weeds present in the soil seed bank (Enache & Ilnicki, 1990; Walker et al., 2004) and reducing soil erosion (Gristina et al., 2009; Novara et al., 2011). Ultimately, being an annual, it will set seeds, die, and dry out at the end of the growing season, exerting no competition with any germinating target plant seedlings the following year. The resulting dry plant biomass of *T. subterraneum* should be

incorporated later into the soil to improve desired properties, such as soil texture, structure, OM, carbon, nitrogen, etc. Practically the dried biomass could be incorporated into the soil by trampling via small domestic ungulates (goats or sheep). Such a grazing pattern would perform a dual purpose: (1) Trampling encourages light incorporation of *T. subterraneum* dry biomass (as a source of OM) into the top 10 cm soil layer, and (2) Increase various forms of nitrogen in the soil by the defecation and urination of animals, permitting even more soil N-enrichment (Semmartin et al., 2010)- being a chronically deficient element in quarry soils. At the initiation of the second growing season, the seed mixture intended for restoration could ultimately be introduced. It is worth commenting that during the second growing season, any germinated *T. subterraneum* seeds would naturally subside in the presence of perennials and annual grass that would compete with the clover for water (Dear & Cocks, 1997).

Finally, it is worth highlighting that although *T. subterraneum*, as a geocarpic plant (Falistocco et al., 1987), can self-plant its own seeds, no concerns of invasiveness are expected since it is a native plant. One drawback arising from using *T. subterraneum* as a pure stand is the temporal creation of a region with low biodiversity due to the growth of an individual plant species over the whole growing season in the restored area.

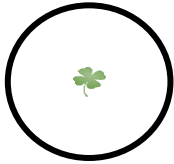
Conclusion and perspectives

This study, performed under ex-situ conditions, could help formulate better comprehension of plant-plant associations. Such interactions can not only assist in the observation of plant communities in semiarid Mediterranean grasslands but might also shed light on the use of native plants (from that same habitat) as nurse plants to facilitate the rehabilitation of degraded systems. The outcomes showed that competition, rather than facilitation, dominated the interaction amongst the studied plant species, resulting in heterogeneous responses amongst different species based on various measured traits. Nevertheless, it is possible to conclude that such manipulations could be another meaningful advancement in fundamental and experimental research. When it comes to conservation and restoration processes, such results are also interesting since they could provide diverse ways for detecting potential nurse plant species capable of increasing the successional dynamics of a plant community. Finally, it is worth noting that although ex-situ studies cannot substitute in-situ experimentations, studies of this kind can

be the initial steps towards selecting different designs, management methods, and species to utilize in any ecological restoration procedure, with lower costs than in-situ settings.

Illustrations - Tables

Illustrations



a. *Trifolium subterraneum* alone



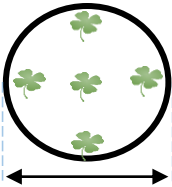
b. *Trifolium subterraneum* + 4 Target plants of same type

(*Aegilops triuncialis* OR *Echinops viscosus* OR *Eryngium creticum* OR *Hyoscyamus aureus*)



c. 4 target plants of same type alone

(*Aegilops triuncialis* OR *Echinops viscosus* OR *Eryngium creticum* OR *Hyoscyamus aureus*)



Pot D. 33 cm

d. *Trifolium subterraneum* + 4 target plants of *Trifolium subterraneum*

Illustration 2. 1. Experimental design, plant arrangements in pots.

Tables

Plant Species	Seed Tested #	Germinated Seeds #	Germination %
<i>Aegilops triuncialis</i>	130	118	90.77
<i>Echinops viscosus</i>	130	126	96.62
<i>Eryngium creticum</i>	130	80	61.54
<i>Hyoscyamus aureus</i>	130	125	96.15
<i>Trifolium subterraneum</i>	130	118	90.77

Table 2. 1. Seed germination percentages based on coleoptile emergence as a proxy of germination under controlled laboratory conditions during an 8 weeks period.

Soil Type	df	F	P-value	Reference soil at time of set-up	Reference soil without soil improvement - TS	Degraded soil at time of set-up	Degraded soil without soil improvement - TS
Clay (g/Kg soil)	3	36.44	< 0.001	209.6 ± 9.8 a	246.6 ± 8.2 b	251.2 ± 14.6 b	330.6 ± 3.0 c
Fine Silt (g/Kg soil)	3	1.18	0.35	324.4 ± 5.0 a	364.8 ± 4.0 a	388.2 ± 12.7 a	305.6 ± 67.1 a
Coarse Silt (g/Kg soil)	3	40.39	< 0.001	117.4 ± 2.7 a	81.4 ± 3.8 b	116.7 ± 4.9 a	66.5 ± 2.7 b
Fine Sand (g/Kg soil)	3	52.80	< 0.001	145.0 ± 5.5 a	121.6 ± 5.1 b	101.0 ± 5.2 c	81.4 ± 0.8 c
Coarse Sand (g/Kg soil)	3	39.10	< 0.001	203.8 ± 7.7 a	185.6 ± 6.5 a	143.2 ± 17.4 b	149.4 ± 3.7 c

Table 2. 2. Results of physical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up, and with the different treatments applied in the pots to the degraded soil without soil improvement. TS is *Trifolium subterraneum*.

Soil Tests Performed	df	F	P-value	Degraded soil at time of set-up	Degraded Soil without soil improvement +TS	Degraded Soil with soil improvement + TS	Degraded Soil with soil improvement +TS + TR	Reference soil at time of set-up
CEC (meq/100gsoil)	4	19.8	<0.001	14.7 ± 0.5 a	13.8 ± 0.3 a	11.5 ± 0.4 b	11.5 ± 0.5 b	12.16 ± 0.2 b
pH Water	4	51.6	<0.001	8.6 ± 0.03 a	8.3 ± 0.05 b	8 ± 0.03 c	8.1 ± 0.03 c	8.4 ± 0.02 b
pH KCl	4	4.4	0.01	7.8 ± 0.02 a	7.8 ± 0.02 a	7.8 ± 0 ab	7.8 ± 0 ab	7.74 ± 0.02 b
Total Carbonates	4	11	<0.001	68.2 ± 0.4 a	72.2 ± 0.5 a	51.4 ± 4.7 b	69.4 ± 0.7 a	71.4 ± 0.4 a

Total Dried Biomass	4	20.5	<0.001	0.8 ± 0.02 a	0.85 ± 0.02 a	1.39 ± 0.1 bc	1.2 ± 0.1 b	1.63 ± 0.03 c
P ₂ O ₅ Olsen (mg/Kg Soil)	4	83.9	<0.001	34.8 ± 0.4 a	42.8 ± 1.4 b	50.2 ± 1.5 c	45.6 ± 0.2 b	58.6 ± 0.4 d
K ₂ O (mg/Kg Soil)	4	28.3	<0.001	300.2 ± 4.6 a	192.2±20.8 bc	221.4 ± 5.7 c	166.8 ± 1.4 b	313.6 ± 7.7 a
MgO (mg/Kg Soil)	4	99.8	<0.001	461.6±9.1ab	440.8 ± 8.8 a	468.2 ± 5.3 b	448.8±1.4 ab	325 ± 4.1 c
CaO (mg/Kg Soil)	4	15.4	<0.001	11140±80.5a	9991.2±216.1b	10999.8±56.3 a	10828 ± 26 a	10962±79.1a
Na ₂ O (mg/Kg Soil)	4	198.3	<0.001	21.8 ± 0.4 a	90.4 ± 14.4 b	231.6 ± 9.2 c	192.4 ± 3.2 c	18 ± 0.8 a
N total (mg/Kg Soil)	4	52.5	<0.001	560 ± 4 a	559.6 ± 36.8 a	692 ± 36.9 b	659.4±26.4ab	1068.2±27.7 c
Carbon (mg/Kg Soil)	4	20.5	<0.001	4.6 ± 0.1 a	5.0 ± 0.09 a	8 ± 0.7 bc	7 ± 0.8 b	9.5 ± 0.2 c
C:N ratio	4	4.7	0.008	8.3 ± 0.2 a	9.1 ± 0.7 ab	11.6 ± 0.8 b	10.5 ± 0.8 ab	8.9 ± 0.4 a

Table 2. 3. Results of chemical soil analyses performed for in-situ degraded soils and in-situ reference soils at time of set-up, with the different treatments applied in the pots to the degraded soil without soil improvement, and after soil improvement. TS is *Trifolium subterraneum*- TR is Target plants.

INTERMEDIATE SECTION

Plant species used in the experiments described in Chapters 2 & 3.

Potential nurse plants used in the experiments

Trifolium subterraneum L.

Fabaceae

Subterranean clover

[Picture: Shaiban, IMBE]



Melica inaequiglumis Boiss & Bl.

Poaceae

Unequal- glumed melica

[Picture: Shaiban, IMBE]



Neighbor Plants

Aegilops triuncialis L.

Poaceae

Barbed goat-grass

[Picture: Shaiban, IMBE]



Echinops viscosus (Boiss.) Feinbr

Asteraceae

Viscous globe- thistle

[Picture: Google Images]



Eryngium creticum Lam.

Apiaceae

Cretan eryngo

[Picture: Google Images]



Hyoscyamus aureus L.

Solanaceae

Golden henbane

[Picture: Shaiban, IMBE]



TRANSITION TO THIRD PAPER

The previous chapter highlighted the employment of a native species (*T. subterraneum*) as a potential nurse plant to assist in restoring a Mediterranean grassland in a former quarry. Nevertheless, results of a 2-year experiment (implemented in a semi-controlled interspecific interaction setting) revealed that competition, rather than facilitation, was the net outcome amongst the experimented plants. However, planting in two consecutive seasons while incorporating dried plant debris into the soil after the first season could render *T. subterraneum* useful in practical restoration- ultimately reducing competition against target species.

Taking what preceded one step further would automatically give rise to some legitimate questions concerning the complexity, or considering the prior situation, the simplicity of such systems, especially when compared to natural existing plant habitats. In natural habitats, plant interactions are usually more complex and dynamic in nature, with several different plant species of various plant populations interrelating and are ameliorated or mitigated by diverse environmental factors such as soil type, water availability, light quality, and temperature fluctuations. All those factors act on a plant along with other plants present in their vicinity- whether of the same or different species. In the coming section, and to replicate the complex plant-natural habitats more satisfactorily, plant species in the experimental design were varied, increased, and differed in planting periods and soil type. Sequentially, shifting from a mono-plant design into three- scenarios of low, medium, and high complexities. Where low complexity is one different plant species in the vicinity interacting with the nurse plant, medium complexity would be three species, and high complexity four species in the nurse plant vicinity. Furthermore, planting at two different time intervals and in two different soil types, a degraded and a reference.

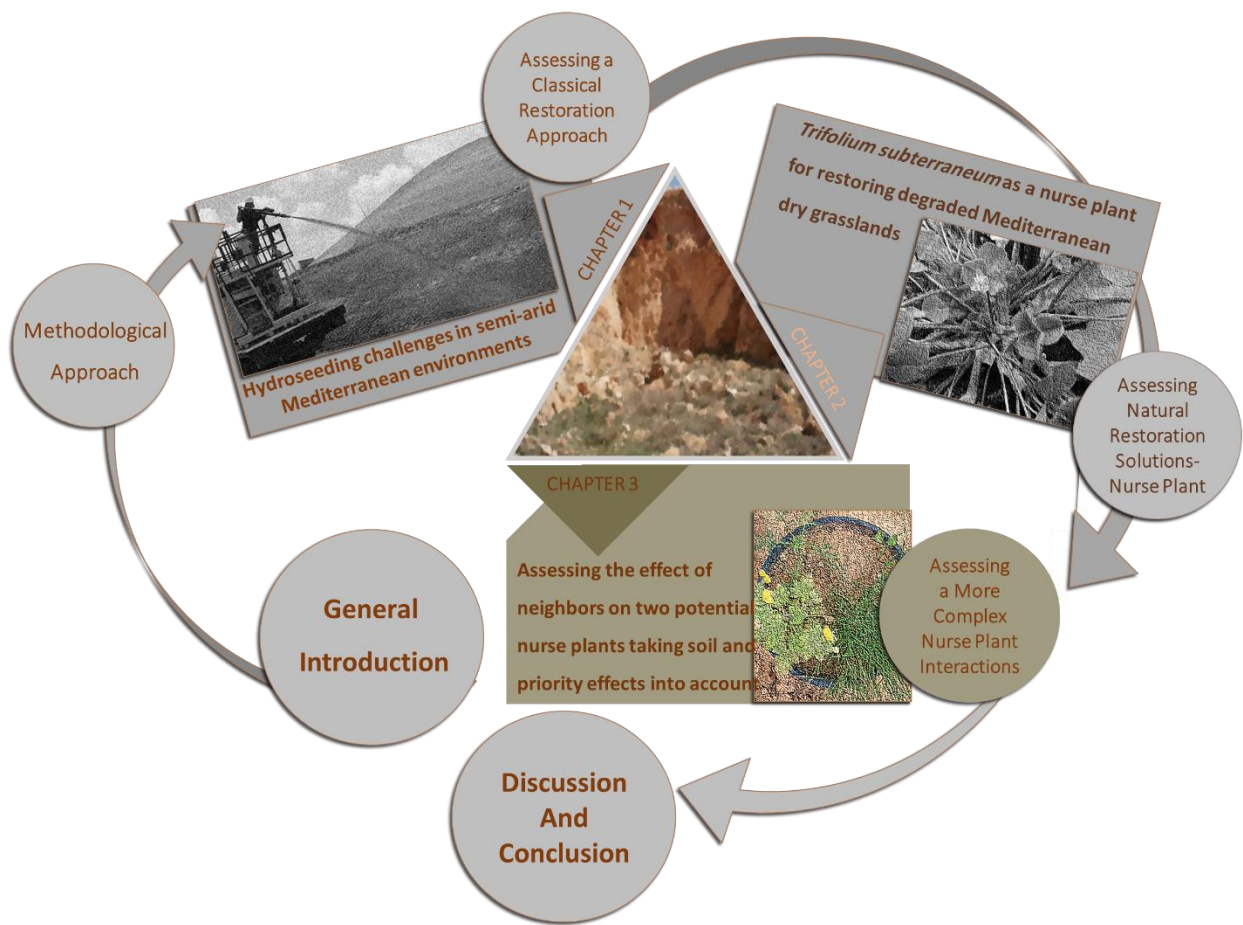


Figure M. 3. Location of chapter three in the general organization of the thesis.

CHAPTER THREE

Assessing the effect of neighbors on two potential nurse plants taking soil and priority effects into account

Results from a semi-controlled interspecific interaction experiment

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In preparation for Applied Vegetation Science

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Abstract

Aim

The potential restoration of an abandoned quarry in the Beqaa plain- Lebanon, into a more sustainable habitat centered on nature-based solutions were evaluated. The experiment assessed whether facilitation or competition was the dominating end result of two potential native nurse plants, a legume (*Trifolium subterraneum* -Fabaceae) and a grass (*Melica inaequiglumis* -Poaceae), with respect to four native co-existing herbaceous plants, from the degraded ecosystem, used as neighbor species in an ex-situ setting. The assessment was performed by evaluating the contribution of nurse plants on plant growth measured by the shift in the above-ground biomass of vegetative parts at four neighboring community levels.

Method

In a 1-year mesocosm experimental setting, the interactions between two potential nurse plants (*T. subterraneum* and *M. inaequiglumis*) and four co-existing species (*Aegilops triuncialis*, *Echinops viscosus*, *Eryngium creticum*, and *Hyoscyamus aureus*) present in the Mediterranean grasslands of Lebanon were separately measured. The planting scheme carried out in soils collected from a former quarry and a nearby reference dry-grassland, had two paths. Under the first path, the initial planting of one potential nurse plant, either *T. subterraneum* or *M. inaequiglumis*, succeeded forty-five days later by planting 1, 3, or 4 individuals of different target species around the nurse plant-indicating varied plant community complexities. In a second scheme, the same nurse plants (also planted independently) were simultaneously planted beside target plants. Additionally, an extra factor considered was replicating the same experiment on two different soil types (from reference or degraded soil).

In both experiments, target plants were planted at different plant community complexity levels: (1) a community composed of only one individual of a single species tested against both nurse plants (separately), (2) a community composed of one individual of three different neighbor species, planted with one of the two potential nurse plants, (3) a community composed of one individual of four different neighbor species, planted with one of the two presumed nurse plants (*T. subterraneum* or *M. inaequiglumis*), (4) a community composed of four individuals of the same type like the nurse plant.

The indices of Relative Interaction Intensity (RII), were calculated for above-ground biomass, total height, and surface area of the vegetative parts. These measurements enabled measuring the plants' competitive ability among different types of soils for the two temporal variations in the experiment (when planting nurse plants 45 days before or at the same time with neighbor plants).

Important Findings

Investigating the effect of neighbor plants on *T. subterraneum* revealed significant competition, evident through negative biomass results, especially in the reference soil. Furthermore, the effect of neighbor plants, regarding planting time and the soil type on *T. subterraneum* biomass also revealed a negative impact on biomass, standing highest when both nurse plant and neighbor were planted together in reference soil at day 0. As for the nurse plant *M. inaequiglumis*, when neighbor plants were introduced at two different dates (0 & 45 days), they revealed moderate facilitation towards the grass *M. inaequiglumis* when given 45 days head-start on neighbor plants in degraded soil.

Conclusion

Both tested nurse plants *T. subterraneum* and *M. inaequiglumis* could aid in restoration practices when introduced in suitable soil type and when priority effect is considered with respect to the other plant species planned for restoration.

Keywords: *Trifolium subterraneum*, *Melica inaequiglumis*, nurse plant, facilitation, competition, soil properties, target plants.

Introduction

Plant interactions are considered key factors that intensely affect the composition and structure of plant communities (Roughgarden & Diamond, 1986). The comprehension of the dynamic nature of complex plant communities has long attracted ecologists for their potential in shaping distribution patterns and traits of involved plant species (Tansley, 1917; Clements et al., 1929; Raffl et al., 2006; Suter et al., 2007). Dynamic assembling could shape plant communities along different trajectories based on plant type, identity (Bakker & Wilson, 2001), quantity, and relative abundance (Grime 1998; Chapin et al., 2002; Grime, 2006), as well as based on varied abiotic conditions (Inouye & Tilman, 1988; Tilman, 2020), such as light, temperature, wind, water, pH, etc. (Wilson & Agnew, 1992). Numerous contradicting scientific literature highlighted either competition (Silvertown & Dale, 1991; Goldberg & Barton, 1992; Goldberg, 1996; Connolly, 1997; Aerts, 1999) or facilitation, governing plant communities (Callaway, 1995; Callaway & Walker, 1997).

For a lengthy period, competition, as an ecological concept, has been regarded as the principal driver of plant community assembling, especially since plant species exploit the same essential limited assets that will ultimately get scarcer (Scott, 2009). Facilitation, as a concept, was neglected and dropped from mainstream ecology for years, endorsing the competition theory (Grime, 1974; Tilman, 1982). Notably, from the late twentieth century onwards, the facilitation concept regained momentum as a plausible interaction shaping plant communities.

In herbaceous plant communities, the role of grasses as nurse plants facilitating other plant species is controversial in the literature. Some studies highlighted facilitation, especially for grasses with shallow roots (Jordan & Nobel, 1979; Franco & Nobel, 1988). Furthermore, facilitation by grass was also documented in degraded semiarid steppes, where the grass *Stipa tenacissima* had a positive role in shrub establishment (Maestre et al., 2001). Facilitation was also demonstrated in mildly-degraded grassland ecosystems (Ren & Liu, 2008), where *Neyraudia montana*, a pioneer grass, ameliorated the microhabitats for neighbor plants. Whereas on the contrary, other research documented competition as the net outcome in the vicinity of grasses, especially among those with dense fibrous roots in the upper soil profile. Also, grasses with a large root-to-shoot ratio permit them to compete efficiently for different soil resources (Caldwell

& Richards, 1986), successfully competing against woody-plant seedlings (Scholes & Archer, 1997). Various studies also noted (e.g., Goldberg et al., 2001; Pywell et al., 2003) that grasses, among diverse herb groups, have more negative significant effects and are stronger competitors than forbs.

Whereas the role of grasses in facilitation is controversial, that of legumes is more apparent, inclining towards facilitation. In arid (Arriaga et al., 1993) and semiarid regions, almost one-third of all nurse plants are from the legume family, with nitrogen-fixing capabilities thru a symbiotic relationship with root-nodulating bacteria (Flores & Jurado, 2003), leading to an enhancement in soil nitrogen availability (Barnes & Archer, 1996) and an improvement in soil nutrient content (den Hollander & Bastiaans, 2007). This characteristic is crucial in Mediterranean soils, which are chronically scarce in nitrogen (Alpert & Mooney, 1996). Consequently, one way to mitigate this mounting situation on plants could be by utilizing self-sowing legume species that can grow and persist (Carneiro, 1999), acting as nurse plants to improve the survival and growth of other species (Padilla & Pugnaire, 2006).

The semiarid Mediterranean ecosystem is characterized by distinct annual climatic sequences, a humid (cool to cold) period lasting 5-10 months (from fall through winter), with mean annual precipitation of more than 300 mm/year (Deitch et al., 2017), pursued by a mild spring, followed by a dry-hot summer (Specht & Moll, 1983). Harsh environmental conditions, scarce water availability, and limited nutrients (mainly nitrogen) are principal abiotic forces responsible for shaping plant communities in such ecosystems (Noy-Meir, 1973; Seligman & van Keulen, 1989; Vilà & Sardans, 1999). Consequently, any stress-mitigating factor, such as natural patchy vegetation distribution (Noy-Meir, 1973; Maestre & Cortina, 2005) - a typical characteristic in a semiarid Mediterranean environment - could enhance plant performance. Shrub and grass species, naturally distributed and developed in such patches, could constitute what is known as 'fertility islands' (Garner & Steinberger, 1989) or 'resource islands' (Reynolds et al., 1999). If assuming that facilitation occurs when benefits exceed competition effects (Holmgren et al., 1997), plants in such islands might induce this facilitation in their microenvironments by enhancing environmental conditions and generating favorable microhabitats (Cortina et al., 2011). This is accomplished by creating those "hot spots" while serving as key elements in

community structures and dynamics for species diversity (Pugnaire & Lázaro, 2000). Positive interactions among different species might be between guilds (such as a nurse tree and its understory species) or within guilds (amongst understory species) (Callaway et al., 1991; Callaway, 1995; Weedon & Facelli, 2008).

More than a third of the world's ecosystems have been modified for subsistence uses by humans, such as cities and agricultural lands. Furthermore, at least another third is already seriously degraded through fragmentation, unsustainable harvest, exotic species invasions, or pollution (Reid, 2005). The United Nations Environment Program has highlighted that restoration of degraded ecosystems is a major global priority, declaring the decade 2021–2030 as the decade of ecosystem restoration (United Nations General Assembly, 2019), emphasizing that ecosystem restoration is among the most profitable public investments for economic growth (Nellemann & Corcoran, 2010). Ecological restoration is promptly becoming an acknowledged complementary conservation action (Young, 2000), aiming toward natural resources in aquatic and terrestrial environments (Reid, 2005).

One nature-based solution used as a tool for ecological restoration involves using specific plants to support other plants or seedlings in what is known as 'Nurse Plant Syndrome'. The concept, investigated at first by Niering et al. (1963), describes plants with positive 'nursing' effects on seedlings beneath their canopy compared to those existing in adjacent areas. Therefore, a nurse plant can buffer non-optimal environmental conditions such as water-limited environments (Niering et al., 1963), intercept rainfall (Padilla & Pugnaire, 2006), improve stressful abiotic conditions (Bertness & Callaway, 1994), reduce radiations, ameliorate extreme temperatures (Flores & Jurado, 2003), create shade alleviating thermal effect, reduce soil water evaporation (Domingo et al., 1999; Pugnaire et al., 2011), act as windbreakers (Walker et al., 2007), mitigate frost effects (Padilla & Pugnaire, 2006), increase seed arrival and trapping (Giladi et al., 2013), supply nutrients and stock water (Holzapfel & Mahall 1999; Flores & Jurado, 2003), protect against grazing (Padilla & Pugnaire, 2006), enhance soil chemistry by symbiotic interactions with soil mycorrhiza (Cuenca & Lovera, 1992), lure pollinators, protect from herbivores, or improve soil quality under their canopy (Callaway, 1995).

In the previous chapter, the experiment - performed under ex-situ conditions - established that competition, rather than facilitation, dominated interactions amongst *T. subterraneum*, as a potential nurse plant, and various neighbor plant species (particularly *Eryngium creticum*, *Echinops viscosus*, *Hyoscyamus aureus*, and *Aegilops triuncialis*). However, *T. subterraneum*, like almost all nitrogen-fixing plants, flourished in degraded soils (even at low nutrient levels), competing with neighbor plants. Nevertheless, when cultivated as a pure stand to be later incorporated as dry organic matter into the soil, *T. subterraneum* improved soil chemical properties by ameliorating total soil organic matter, nitrogen, and phosphorous, consequently exhibiting moderate facilitative impact on other plant species. Accordingly, from a practical restoration perspective, *T. subterraneum* could be endorsed for re-establishing soil fertility in degraded quarries. Though, it should be seeded initially as a pure stand the first year. Later, in the second year, its dried biomass (produced at the end of the growing season) could be incorporated into the soil by small domestic ungulates trampling before seeding the mixture intended for restoration (*Shaiban et al.*- in preparation, chapter 2 of this document).

Nevertheless, under in-situ conditions, interactions amongst plants in communities, whether competition or facilitation, is way more complex. Such interactions are not simply between populations of two different plant species but involve several plant species at varying complexity levels (species composition, population densities, spatial and temporal separation, phenology, etc.). This paper aims to evaluate the possible use of two potential nurse plants type (an annual legume - *Trifolium subterraneum* – Fabaceae, and a perennial grass - *Melica inaequiglumis* - Poaceae) in an ex-situ setting with respect to different soil types (degraded versus reference soil), different categories of micro- plant communities complexity levels (composition, species richness, family diversity, and spatial distribution), and finally, with differences based on planting time effect (to test potential priority effect- check the subsequent paragraph). Ultimately, to support the restoration of soil and vegetation of a longstanding degraded and abandoned quarry present in the Mediterranean dry grassland in comparison with non-degraded soil by former quarry exploitation (reference soil).

Priority effects

Priority effects are those results induced by the order in which species reach a particular site exercising a significant role in community assembly. Consequently, early arriving colonizers alter the performance of later ones (Hess et al., 2019) by affecting the establishment, survival, development, or proliferation of later-arriving species (Helsen et al., 2016). This impact could be a negative one, through the reduction of available resources such as space, light, and nutrients (Vance, 1984), or have a positive impact, especially in harsh environments with extreme solar radiation, severe temperatures, or unstable substratum. Accordingly, any absence of such earlier colonizers might lead to lower success chances for late-arriving native plants (D'Antonio & Meyerson, 2002). In literature, numerous publications documented that allowing native species a head-start (one to several weeks) was adequate to substantially reduce invasiveness in grassland (Grman & Suding, 2010; Vaughn & Young, 2015; Young et al., 2016), with success up to 85% in some cases (Suding, 2011).

Materials and Methods

The number of neighbor species comprised different neighbor community complexity levels, ranging from, (1) a neighbor community composed of only one individual of a single species (*Echinops viscosus*) planted with one of the two tested nurse plants (*T. subterraneum* or *M. inaequiglumis*) or (2) a neighbor community composed of one individual of three different neighbor species (*Aegilops triuncialis*, *Echinops viscosus*, *Hyoscyamus aureus*), also planted with one of the two potential nurse plants (*T. subterraneum* or *M. inaequiglumis*), or (3) a neighbor community composed of one individual of four neighbor species (*Aegilops triuncialis*, *Eryngium creticum*, *Echinops viscosus*, *Hyoscyamus aureus*), planted with one of the two presumed nurse plants (*T. subterraneum* or *M. inaequiglumis*), (4) a neighbor community composed of four individuals of the same type as the nurse plant, and finally, (5) the nurse plants established each alone in the pot (Illustration 3. 1.). The purpose was to test the effect of neighbor plants on the biomass of both potential nurse plants *T. subterraneum* and *M. inaequiglumis* for assessing the effects of plant community complexity on the potential facilitation or competitive effects of the two potential nurse species tested in complement of experiment one which was only performed for one specific level with four individuals of each neighbor species.

Nurse plant species used

The perceived nurse plants assessed were *Trifolium subterraneum* - Fabaceae (an annual legume plant species) and *Melica inaequiglumis* - Poaceae (a perennial grass plant species), both native to the Mediterranean plant community and have a significant functional role.

***Trifolium subterraneum* (Fabaceae)**

T. subterraneum (Fabaceae- Subterranean clover); tribe Trifolieae (Zohary & Heller, 1984) is a self-sowing legume native to the Mediterranean. A multi-stemmed annual plant (Figure 3. 1a), ranging in length from 5-45 cm and growing on dry soils in open plains and mountains, from sea level up to 1800 m.a.s.l. (Ecocrop, 2017), germinating and establishing during the cool and wet season (Buddenhagen, 1990), flowering in March-April, and setting fruits -in the form of pods- in April-May (Vasileva et al., 2016). The self-sowing process is possible through a well-known mechanism termed 'active geocarpy' (Zohary, 1962), permitting plants to actively bury their seeds (Barker, 2005), resulting in seed dispersal within a short distance from the mother plant. This process occurs when a newly created flower head penetrates the soil (Falistocco et al., 1987) and transforms into a completely-buried 10–15mm elliptical one-seeded skin-like pod. A classic example of geocarpy is present in the peanut plant *Arachis hypogaea* L. (Kaul et al., 2000). Subterranean clover is a species with high ecological flexibility, evident in its presence in a vast habitat that ranges from sparse oak forests to pastures of varied slopes (Vasileva et al., 2016). It is also a versatile plant used for weed suppression, green manure, mulching substance, grazing (Clark, 2007), and erosion control (Howieson et al., 2000). It also has N-fixing capabilities (Ferreira & Castro, 2005) due to its symbiotic relationship with *Rhizobium leguminosarum* biovar. trifolii bacterial species, or with vesicular-arbuscular mycorrhizas enabling the fixation of around 50 to 188 kg/ha of nitrogen/year (Sanford et al., 1994; Bolger et al., 1995).

Figure 3. 1. Potential nurse plants used in the experiment.



(a) *Trifolium subterraneum*. (Shaiban, IMBE)

(b) *Melica inaequiglumis*. (Shaiban, IMBE)

Melica inaequiglumis* (Poaceae) syn. *Melica persica* ssp. *inaequiglumis

With a distribution range covering almost all of the planet except the tropical regions and Australia, the genus *Melica* L. comprises about 80 perennial sp. of rhizomatous grasses (Clayton & Renowitz, 1986). The species *M. inaequiglumis* (Figure 3. 1b), found in central Asia, India, and China (Hadi et al., 2019), is also native to Lebanon (Tohmé & Tohmé, 2014). It is a caespitose rhizomatous, deciduous perennial grass that forms dense clumps and flowers from late spring into late summer (Clayton et al., 2012). *M. inaequiglumis* thrive in full sun, dry locations, grassy hillsides, steep slopes, and rocky areas from 1500-4900 m.a.s.l. (Hadi et al., 2019). A deep well-spread root system with abundant root hair enables the wide adaptation of this pioneer species to rocky, volcanic, and limestone soils under extreme climatic variations, such as prolonged drought and severely cold temperatures. All those qualities make *M. inaequiglumis* noteworthy as a plant species for soil and moisture conservation (Kumari & Saggoo, 2016).

Neighbor species

Neighbor plant species used in the study were *Aegilops triuncialis*, *Echinops viscosus*, *Eryngium creticum*, and *Hyoscyamus aureus*. All are abundant species often present in degraded areas during early succession stages (Khater et al., 2004), and accordingly could be regarded as representative species of reference ecosystems suitable for reintroduction in degraded areas,

such as abandoned quarries. Furthermore, the seeds of these species are easy to collect, store well, and are unfussy and reliable in germination.

***Aegilops triuncialis* L.**

The *Aegilops* genus belongs to the Triticeae tribe, within the Pooideae subfamily, in the Poaceae family. The *Aegilops triuncialis* species (Figure 3. 2d) has the widest distribution inside the genus (Maxted et al., 2008), extending from Asia into the Mediterranean Basin and throughout southern Europe. The species, predominantly found in limestone and basalt, is abundant in different habitats ranging from dry and partially disturbed to dry-rocky slopes, cultivated fields and surrounding edges, matorrals, grasslands, shrublands, woodlands, and open forests. *A. triuncialis* is also present in steppes, desert margins, river terraces, and seashores. It grows from sea level up to 2,700 m.a.s.l., under a wide range of annual rainfall, from 125 mm to 1,400 mm (van Slageren, 1994).

***Echinops viscosus* L.**

With approximately 120 species distributed all over the world (primarily in the Northern Hemisphere), the genus *Echinops* L. (Asteraceae, Cardueae) (Garnatje et al., 2004a) is predominantly a perennial, with very few annual species (Garnatje et al., 2004b). The species *Echinops viscosus*, synonyms including *E. spinosissimus* subsp. *macrolepis* (Boiss.) Greuter, *E. viscosus* subsp. *macrolepis* (Boiss.) Feinbrun, *E. viscosus* DC. var *macrolepis* Boiss., *E. syriacus* Boiss (common English name: Viscous Globe Thistle), is categorized by uni-flowered capitula aggregated into second-order spherical or oval heads, this syncephalia being a unique feature within the tribe (Petit, 1997). *E. viscosus* is a spiny perennial herb, 80-100 cm tall plant flowering from May till August (Figure 3. 2c). In Lebanon, it is present in sunny plots in several locations ranging from fields, roadsides, abandoned lands, dry and rocky slopes, and scrublands (Arnold et al., 2015).

***Eryngium creticum* Lam.**

With nearly 250 species, the genus *Eryngium* is regarded as the largest and the most taxonomically complex in the Apiaceae family. Distributed in the temperate regions of every continent (Calvino et al., 2008), it is differentiated from other Apiaceae members by the presence of a single bract per flower and a capitate inflorescence (Calvino et al., 2008). The

species *Eryngium creticum* Lam. (Common English name: Field Eryngo) is a spiny perennial, occasionally a biennial or an annual, glaucous and glabrous herb, with an erect and branched stem reaching up to 50 cm in height. The plant has sessile and palmately divided 3–8 prickly lobed leaves, flowering from May till August (Kikowska et al., 2016) (Figure 3. 2b). It is present in various types of dry and damp soils on hillsides, cultivated or abandoned lands, and cliff crevices (Arnold et al., 2015). In the eastern Mediterranean regions, it is frequently found in sunny locations at low altitudes throughout Lebanon, Palestine, Jordan, and Syria (Kikowska et al., 2016).

***Hyoscyamus aureus* L.**

A small herbaceous, uni-regional genus, the *Hyoscyamus* includes 20 species, occupying Europe, northern to north-eastern Africa, and the phytogeographical Sino-Japanese region (Nasir, 1985). The *Hyoscyamus aureus* (Golden Henbane) (Figure 3. 2a) is a glandular-villous perennial plant species with a golden yellow corolla having a purple throat. The species is present in several eastern Mediterranean countries such as Turkey, Cyprus, Lebanon, Iraq, Syria, Israel, Jordan, and Egypt (Brandes, 2002). *H. aureus* plants still grow on the old citadel walls of Jerusalem, where its pollen, along with pollen of other plant species, has been identified within the famed Shroud of Turin (Frei, 1983).

Figure 3. 2. Neighbor plants used in the experiment. (Shaiban, IMBE).



(a) *Hyoscyamus aureus*

(b) *Eryngium creticum*

(c) *Echinops viscosus*

(d) *Aegilops triuncialis*

Experimental design

The experiment aimed to achieve the following: (1) test the effect of neighbor plants on two potential nurse plants – *T. subterraneum* (Fabaceae) and *M. inaequiglumis* (Poaceae); (2) test the contribution of soil properties (degraded ecosystem vs. reference Mediterranean dry grassland) on plant interactions; (3) test whether there are any significant priority effects between nurse plants and neighbors by either growing them together (at the same time- day 0) or separately (nurse plant planted 45 days earlier than neighbor plants); (4) test the effect of four different plant communities: one individual of one neighbor species; one individual of three neighbor species; one individual of four neighbor species; four individuals of one species similar to nurse plant species (Illustration 3. 1.).

Soil collection

The required soil for the mesocosm experiment, collected from a quarry (composed of reefal and dolomitic limestone), was considered the degraded ecosystem (Figure 3. 3a) existing near the small village of Maqneh in eastern Beqaa plain- Lebanon (Figure 2. 3.). The non-degraded soil, considered the reference ecosystem, was taken from the adjacent grazed Mediterranean dry grassland (Figure 3. 3b). This grassland, which lies within the Pre-Steppic Mediterranean Ensemble (MoA/UNEP, 1996), is characterized by the presence of some rare and endemic species (*Campanula euclasta*, *Stachys nivea*, *Alcea damascena*, and *Astragalus roussaeanus*), also specialized steppic species (*Serratula cerinthifolia*, *Convolvulus dorycnium* ssp. *oxysepalus*, *Capparis spinosa* ssp. *Parviflora*, *Parietaria judaica*, *Alkanna orientalis*, *Hyoscyamus aureus*, and *Moluccella laevis*). A bulk volume of 10 cubic meters was removed from both degraded and reference sites and conveyed by truck to the intended experiment location.

Figure 3. 3 The two sites where seeds and soil were collected:



(a) The quarry, considered the degraded site. (b) Nearby grassland as a reference site.
... (Shaiban, IMBE)..... (Shaiban, IMBE)

Seed collection

As documented in scientific literature, local seed populations are superior to non-local ones (Kleinschmit et al., 2004), therefore required seeds for the experiment were collected from the nearest source populations to match the habitat as closely as possible (Vander Mijnsbrugge et al., 2010). The neighbor seed species *Aegilops triuncialis*, *Echinops viscosus*, *Eryngium creticum*, and *Hyoscyamus aureus* were collected by hand, after seed set (Sept. 2018), from the vicinity of the quarry within a radius of 0.2 Km. The collected seeds were conserved in a shady location to dry for one month by natural airflow. Subsequently, they were all placed into properly-closed plastic boxes, and a capsulated volatile insecticide, Naphthalene (C₁₀H₈), was applied to eradicate any insects alive, whether in the larval or adult stage (Romano, 1966). As for the required seeds of both nurse plants, those of *M. inaequiglumis* were collected following the same procedure as the target plants and in the same locality, whereas *T. subterraneum* seeds were imported from Fertiprado-France (5kg sealed bag) because no abundant quantity was locally available. A hundred seeds of each species were sampled for germination percentage in a growth chamber (temperature 15/20 °C, 08/16h-night/day) at the Institute of Mediterranean Biology and Ecology Laboratory in Avignon, France. Coleoptile emergence, used as a proxy of germination, was recorded every 2-3 days for eight weeks (Table 3. 3.).

Mesocosm experimental site

The experiment took place in a south-facing tunnel greenhouse (Figure 3. 4.) in the small village of Zahrieh, in Mount Lebanon, Lebanon (Latitude 33°88'47.9", Longitude 35°70'65.6"), and at an altitude of 700 m.a.s.l.



**Figure 3. 4. The general setup of the mesocosm experiment in a tunnel- greenhouse.
(Shaiban, IMBE)**

Soil preparation and analyses

Collected soil, shoveled from the top 5-10 cm layer of both degraded quarry and adjacent reference grassland (Figure 3. 5a, b), was moved to the intended experimental location, sieved through a 2-mm sieve mesh (Figure 3. 5c), mixed with perlite (ratio of 10:1) (Figure 3. 6a), and filled in 15 liters pots (33 cm diameter - 30 cm height). A 3 cm layer of pebbles (size 0.5-1cm) initially added at the bottom was separated from the soil by a Geotextile fabric layer purposed to prevent soil loss while permitting proper water drainage (Figure 3. 6b).

Figure 3. 5. Extraction, transportation, and preparation of soil from reference and degraded sites. (Shaiban, IMBE).



(a) Soil collection at 10 cm depth (b) Soil removal from the site (c) Soil sieving and preparation

Figure 3. 6. Soil preparation, filling, and irrigation installation. (Shaiban, IMBE)



(a) Mixing perlite at a 10:1 ratio (b) Barrier amid pebbles & soil (c) Adding an irrigation system

Ten soil samples, each weighing 100g, were randomly collected from the two sites, the reference ecosystem and the degraded ecosystem (five from each). The collected samples were dried and sieved through a 2-mm mesh to be tested later for physical and chemical characteristics at Teyssier Laboratory (Bordeaux-France). Both reference and degraded soils were analyzed for the following parameters (Table 3. 1.): particle-size distribution in 5 fractions without prior decarbonization (clay less than 0.002 mm, fine silt between 0.002-0.02 mm, coarse silt between 0.2-2 mm, fine sand between 0.05-0.2 mm, and coarse sand between 0.2-2 mm) (Robinson & Friedman, 2003). Furthermore, soil chemical analysis were computed (Table 3. 2.): organic C (Allison, 1965), C: N ratio, total N by dry combustion (Bremner, 1996; Dumas, 1831), plant-available P (Olsen et al., 1954), exchangeable K⁺ (Metson et al., 1956; Ciesielski et al., 1997), CaCO₃- using a Bernard Calcimeter (Sparks et al., 1996), Cation Exchange Capacity (CEC), and pH water ratio 1:5 (Thomas, 1996).

Experimental procedure

To evade potential setbacks during the early seedlings' development phase and minimize weed competition, from seeds present in the soil seed bank of the original soil, all seeds utilized in the experiment were sprouted in germination trays (Figure 3. 7a) in a germination chamber at a temperature of 22/24 °C, 08/16h-night/day. The germination mixture included two parts soil (from either reference or degraded environment) to one-part standard germination medium. After seed germination and growth of the first set of true leaves, all trays were moved to a greenhouse below a 50 % shade net. For three days, they were hardened and acclimatized to fluctuating day and night temperatures while gradually adapting to direct sunlight under greenhouse conditions (Figure 3. 7b). Finally, the seedlings were all transplanted to the designated pots (Diameter 32cm - Height 27cm) situated in full sun (Figure 3. 7c).

Figure 3. 7. Seedling germinating, hardening, and planting. (Shaiban, IMBE)



(a) Germinating seed in trays

(b) Hardening seedlings

(c) Transplanting seedlings to pots

The 232 pots were sub-divided into two equal groups containing 116-pots each. The first group of the 116 pots was further subdivided equally into 58 pots filled with soil from the quarry (degraded ecosystem) and 58 pots filled from the nearby grassland (reference ecosystem). The germinated seedlings of either *T. subterraneum* or *M. inaequiglumis* were transplanted into the pots, along with (1) only one individual plant of *E. viscosus*, (2) three other species (*A. triuncialis*, *E. viscosus*, *H. aureus*), (3) four other species (*A. triuncialis*, *E. viscosus*, *Er. creticum*, *H. aureus*) (Illustration 3. 1.). The second set of 116 pots (of the initial 232 pots) was also equally divided into 58 pots filled with soil from the degraded ecosystem (quarry), and the remaining 58 pots were all filled from the reference ecosystem (nearby grassland). This set of 116 pots was planted equally with either an individual *T. subterraneum* or *M. inaequiglumis* seedling and set aside for

45 days allowing a head-start for the planted seedlings prior to replicating the formerly mentioned procedure (Illustration 3. 2.).

All pots were arranged in a South-facing tunnel-greenhouse on a concrete surface (to eliminate undesired weeds) and spaced at an intra-and inter-row distance of 20 cm. Pots were watered when soil surfaces dried to a depth of 1 cm. The irrigation was through a drip-irrigation system, with one online dripper (adjustable range from 0 to 40 lit/hour) attached by a 2mm spaghetti tube extended from a 16mm Polyethylene irrigation pipe (Figure 3. 6c). The irrigation water, supplied through a pump from an artesian well, was kept in a plastic tank to allow the settling of any soil particles before use. For two weeks before planting, pots were thoroughly watered, permitting the germination of voluntary weeds (from the filled natural soil) to be later removed with minimal soil disturbance. Moreover, throughout the experiment, all undesirable seedlings that germinated were removed.

The experiment followed the competition protocol suggested by Gaudet and Keddy (1988, 1995), hence introducing a various number of seedlings/ pot (1 or 3, or 4 diverse seedlings) of different species (*A. triuncialis*, *E. viscosus*, *Er. creticum*, and *H. aureus* (Illustration 3. 1b, c, d) transplanted equidistantly into either reference or degraded soil type, with half planted at the exact planting date with one of the two tested nurse plant, and the second half at 45 days later (testing priority effect). For statistical significance, all combinations were replicated four times.

Plant measurements

The effect of neighbor plants on the two nurse plants (*T. subterraneum* and *M. inaequiglumis*) was evaluated at the end of the spring season. The timing coincided with the fruit-setting stage before the end of their annual cycle. The indicative functional trait calculated was the above-ground biomass (Gaudet & Keddy, 1988; Rösch et al., 1997; Navas & Moreau-Richard, 2005) achieved by cutting all plants at the soil level, oven-drying at 50°C for 48 hours, and finally weighing them on a digital balance (precision of ± 0.01 grams).

Analyses

Protocol used

The effect of neighbor plants on the phytometers *T. subterraneum* and *M. inaequiglumis* was calculated separately using the Relative Interaction Intensity Index (RII) to compute the plant biomass of the designated phytometers. All measurements taken were with respect to the existence and effect of neighbor plants in different communities, with only one neighbor plant, three plants, and four plants. The RII is the selected tool to calculate those interactions considering it possesses the following statistical and mathematical properties: (1) it is symmetrical with respect to zero, having identical absolute values for competition and facilitation. With a range from 0 to +1 designating 'Facilitation' whereas the range from -1 to 0 designates 'Competition', (2) is linear, and (3) it has no discontinuity within its range (Howard & Goldberg, 2001; Armas et al., 2004; Liancourt et al., 2009).

The RII was calculated according to the following equation:

$$RII_{\text{response}} = \frac{(P_{\text{with } n} - P_{\text{without } n})}{(P_{\text{with } n} + P_{\text{without } n})}$$

Where the RII response was that of the neighbor plant(s) (n) on the Phytometer (P). The phytometers measured were *T. subterraneum* and *M. inaequiglumis*. Whereas the neighbor plants were *A. triuncialis*, *E. viscosus*, *Er. creticum*, and *H. aureus* (Illustration 3. 1b, c, d). Also, the measurement of the RII response of neighbor plants of the same type as the nurse plant was considered only for *T. subterraneum* (Illustration 3. 1e).

Statistical analyses

All analyses were performed with R-3.6.0 (R Core Team 2020). To assess the competitive effect of *T. subterraneum* (ability to reduce the performance by neighbors), two-way ANOVAs or two-way ART ANOVAs (Aligned Ranks Transformation ANOVAs) were performed on the RII_{response} . The interaction of three explanatory variables was tested for (1) the type of soil (reference vs. degraded), (2) the planting time (day0: P and n planted together vs. day45: P planted 45 days before n), (3) the identity of the neighbor species. ANOVAs were applied when

data responded to the hypotheses of normality and homogeneity of variance (RII calculated on *Trifolium* biomass). ART ANOVAs were performed when otherwise (RII calculated on *Melica* biomass) (Mangiafico, 2016). All were followed by pairwise contrast comparisons with a Tukey adjustment when significant. In order to find out if each RII was significant from zero, thus indicating competition or facilitation, a Wilcoxon test was performed on each level of explanatory variables.

Results

Effect of neighbor plants on *Trifolium subterraneum* biomass (RII_{response})

The result of the evaluation of the plant biomass parameter with respect to soil type (reference or degraded) and planting dates (simultaneously planted or 45 days apart) revealed that *T. subterraneum* biomass was affected ($F=9.03$, $p=0.005^{**}$) in a negative manner due to the presence of neighbor plants (Figure 3. 8.), with a significant difference primarily in reference soil, when *T. subterraneum* was planted simultaneously with neighbor plants.

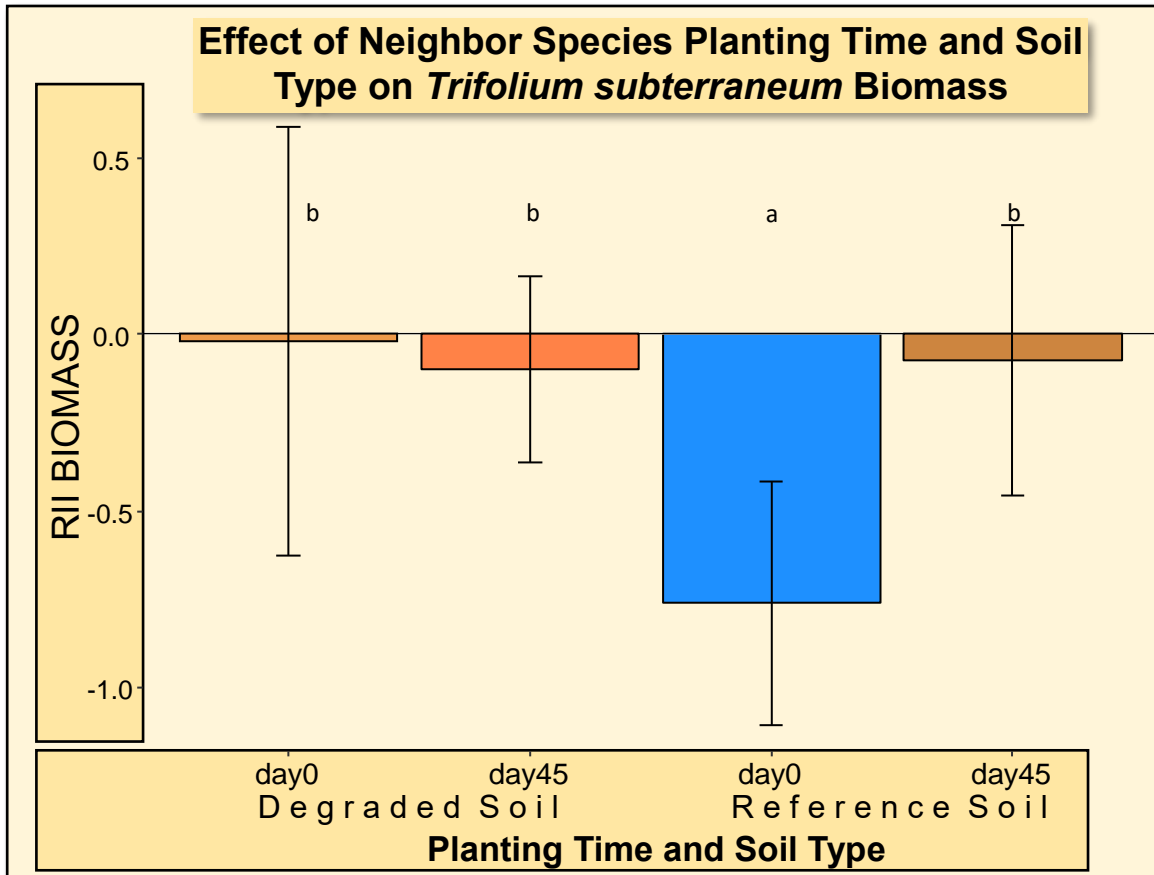


Figure 3. 8. Response of *Trifolium subterraneum* biomass to neighbors affected by the type of soil and planting date ($F=9.03$, $p=0.005^{**}$) ($n=4$). The horizontal line marks $RII=0$, above which positive RII value indicates facilitation and below which negative values indicate competition. Bars sharing a letter were not significantly different from each other ($p<0.05$). Boxplots colored in blue show RII significantly different from 0 (tested by Wilcoxon test).

Effect of neighbor plants on *Melica inaequiglumis* biomass ($RII_{response}$).

The effect of neighbor plants on the RII biomass results for *M. inaequiglumis* showed a negative effect ($F=7.04$, $p=0.014^*$), that was significantly evident on reference soil regardless of sowing patterns and on the degraded soil when the nurse plant and neighbor plants were planted at the same date (Figure 3. 9.)

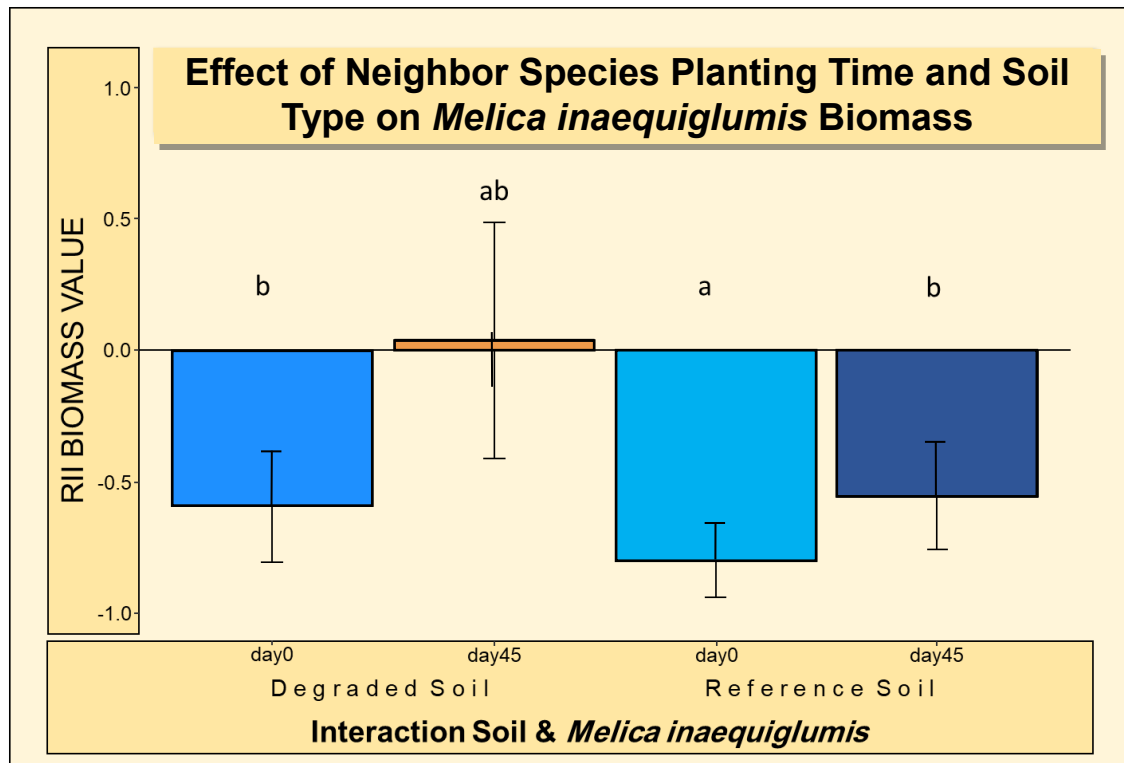


Figure 3. 9. Response of *Melica inaequiglumis* biomass to neighbors affected by the type of soil and planting date ($F=7.04$, $p=0.014^*$) ($n=4$). The horizontal line marks $RII=0$, above which positive RII value indicates facilitation and below which negative values indicate competition. Bars sharing a letter were not significantly different from each other ($p<0.05$). Boxplots colored in blue show RII significantly different from 0 (tested by Wilcoxon test).

Discussion

Although numerous studies in the literature support the positive role of nurse plants in facilitating other plants (Arriaga et al., 1993; Bertness & Callaway, 1994; Bertness & Hacker, 1994; Brooker et al., 2008; Pugnaire et al., 2011), our results fall under the stream of research considering competition, rather than facilitation, as the dominant factor governing interactions amongst different plant species (Ricklefs, 1977; Wilson, 1988; Goldberg & Barton, 1992; Casper & Jackson, 1997; Grace, 2012; Wright et al., 2014).

Effect of neighbor plants on *Trifolium subterraneum* biomass

In the previous chapter, competition (rather than facilitation) was the dominant effect amongst *T. subterraneum*, as a nurse plant, and various neighbor plant species. Nevertheless, when planted in a pure stand in degraded soils (even at low nutrient levels), *T.*

subterraneum flourished. The results of this chapter support previous results, although through a different path - if not from an opposite angle.

Investigating the effect of neighbor plants on *T. subterraneum* revealed competition translated through negative biomass RII values, especially in the reference soil (Figure 3. 8.). Analyzing initial soil test results taken from both reference and degraded soils (Table 3. 2.), permitted a better grasp of the outcome. These soil results showed a higher level of several essential elements in the reference soil when compared to the degraded one. For example, total organic matter was higher in reference (1.63 ± 0.03 meq/100g soil) than in degraded soils (0.8 ± 0.02 meq/100g soil). Phosphorus was higher in reference soil (58.6 ± 0.4 mg/Kg) than in degraded soils (34.8 ± 0.4 mg/Kg), and so was total nitrogen (1068.2 ± 27.7 mg/Kg in reference soil vs. 560 ± 4 mg/Kg in degraded soil). This nutrient abundance in reference soil generated better growth of neighbor plants, exerting more competition towards the nurse plant *T. subterraneum*, ultimately reducing its biomass (Figure 3. 8.). This same fact was apparent, though less, in degraded soil, with lesser but still existing competition, by neighbors on *T. subterraneum*. One possible explanation for this would be the lower nutrients in degraded soil for similar plant growth, resulting in weaker competition towards the nurse plant. Furthermore, being vetch, *T. subterraneum* can perform better in poor soil due to the symbiotic relationships it can establish.

Likewise, the simultaneous effect regarding planting time and the soil type on *T. subterraneum* biomass confirms the above deduction. Where the highest significant negative impact on biomass was evident when both nurse plant and neighbor were planted together in reference soil at day 0 (Figure 3. 9.). Considering the same treatment, still in reference soil, but with a 45 days window between planting *T. subterraneum* and neighbor plants, revealed a much less, though persistent negative effect from neighbors on *T. subterraneum* biomass. Moreover, when compared to those planted in degraded soil at day 0, the biomass results revealed a significant difference. Comparing the impact of neighbor plants on *T. subterraneum* in degraded soil with respect to planting time and soil type at day 0 and day 45 showed a negative effect. Furthermore, these results complement earlier discussions, primarily with neighbor plants growing in poor degraded soil resulting in poor plant growth, unable to affect nurse plant biomass negatively. Finally, there was no effect of neighbor communities on *T. subterraneum* biomass.

Effect of neighbor plants on *Melica inaequiglumis* biomass

A significant effect was evident from the neighbor plants on *M. inaequiglumis* biomass in reference soils when planted together on Day 0 vs. neighbors planted 45 days later (Illustration 3. 2.). The fact that the RII biomass value of *M. inaequiglumis*, planted 45 days earlier, was significantly better (though still negative) reinforces the priority effect concept. Regarding planting in degraded soil, neighbor plants grown 45 days behind the nurse plant exhibited an RII not different from zero (no facilitation nor competition) of neighbors on *M. inaequiglumis* grass (figure 3. 9.). This result highlights the importance of a head-start interval for the *M. inaequiglumis* grass as a nurse plant, especially in poor degraded soils. On the contrary, and yet in degraded soil, *M. inaequiglumis* biomass negative results suggested severe competition when planted the same day as neighbors. This competition could be due to the better efficiency of neighbor plants in utilizing the scarce nutrients available in such soils. Regarding competition for moisture (with perennials developing at a slower rate than annuals), it was not of critical effect in this case simply because (1) all plats were initiated as seedlings, and (2) when required, water was supplied regularly (via direct irrigation), therefore water was not a limiting factor. Finally, and similar to the results of *T. subterraneum*, there was no effect of neighbor communities on *M. inaequiglumis* biomass.

Conclusion and perspectives

Potentials of using *Trifolium subterraneum* as a nurse plant.

Soil is essentially the basis for any intended quarry-restoration endeavor. Therefore, the initial reintroduction of soil as a surface layer is a crucial recovery step in any quarry planned for restoration (Zhang et al., 2018). Soil type, structure, thickness, physical and chemical properties, fertility, and water holding capacity (Oldeman, 1992; Ferreira et al., 2022) matter. Unfortunately, rarely can such characteristics be selected for or are easily manipulated in reintroduced topsoil layers intended for quarry restoration. Evidently, this renders soil tests a much-needed tool for deciding on various restoration strategies. Based on test results (texture, nutrient quantities, availability), a specifically suited restoration strategy could be adopted. One intriguing restoration decision could be the utilization of nurse plants. *However, could such tests assist in*

narrowing down on a specific type of nurse plant to be used? The research performed in Chapter 2, also reconfirmed in this chapter (from a different perspective), envisages such possibilities.

In restoration practices, while bearing in mind the previous overview, it is credible to state that *T. subterraneum*, as a nurse plant, could be a more suitable choice for restoring nutrient-deficient or poor reintroduced topsoil in degraded quarry sites rather than a rich reintroduced soil. This consideration could be due to the following, (1) Considering the fact that *T. subterraneum* flourishes in poor soils, by capitalizing on nitrogen-fixing capabilities, along with results indicating that it might fail to thrive well in nutrient-rich soils amongst other native plants (Figure 3. 8.). Hence, it is imperative to test the soil before utilizing it as a nurse plant for restoration purposes. (2) To ensure it can perform its role as an appropriate nurse plant in restoring soils, the effect of neighbor plants should be delayed (Figure 3. 8.) if considering the priority effect concept- accordingly, separating its planting date from that of its neighbors. This fact overlaps with the results of Chapter 2, revealing that it is more promising to plant it initially alone and later reintroduce the intended seeds for restoration.

Potentials of using *Melica inaequiglumis* as a nurse plant.

As for *M. inaequiglumis*, it could be utilized as a nurse plant (taking into consideration results of the priority effect) by introducing into degraded soil and allowing it to establish solely, preferably for one growing season (since a 45-days-interval provided slight facilitation in degraded soil- Figure 3. 9.), before sowing other seed species purposed for restoration. Established *M. inaequiglumis* plants will conceivably facilitate newly seedlings through the following: (1) As a deciduous perennial grass, *Melica* will go dormant and dry up in mid-summer (Ketabi et al., 2004), leaving behind abundant organic material suitable for degraded soil enrichment along with enhancement of its water holding capacity - Two essential components for newly established seedlings. (2) With an extensive fibrous root system, *M. inaequiglumis* (Poaceae) forms a thick well-spread mat stabilizing and reducing soil erosion (Kumari & Saggoo, 2016), preserving it to the benefit of delicate germinating seedlings. (3) When a new growing season picks up, dormant *Melica* plants (being a caespitose rhizomatous deciduous perennial grass (Clayton et al., 2012)) will re-emerge, develop, and clump, ultimately aiding in protecting and

nourishing any seeds or fragile seedlings in their vicinity (Maestre et al., 2001) through microclimate amelioration (mitigating cold weather, harsh summer sun, dry wind...).

Tables – Illustrations

Tables

Soil Type	Df	F	P-value	Reference soil 2018	Degraded soil 2018
Clay (g/Kg soil)	3	36.44	< 0.001	209.6 ± 9.8 a	251.2 ± 14.6 b
Fine Silt (g/Kg soil)	3	1.18	0.35	324.4 ± 5.0 a	388.2 ± 12.7 a
Coarse Silt (g/Kg soil)	3	40.39	< 0.001	117.4 ± 2.7 a	116.7 ± 4.9 a
Fine Sand (g/Kg soil)	3	52.8	< 0.001	145.0 ± 5.5 a	101.0 ± 5.2 c
Coarse Sand (g/Kg soil)	3	39.1	< 0.001	203.8 ± 7.7 a	143.2 ± 17.4 b

Table 3. 1. Results of physical soil analyses performed for in-situ degraded soils and in-situ reference soils in 2018.

Soil Tests Performed	Df	F	P-value	Degraded Soil 2018	Reference Soil 2018
CEC (meq/100gsoil)	4	19.8	<0.001	14.7 ± 0.5 a	12.16 ± 0.2 b
pH Water	4	51.6	<0.001	8.6 ± 0.03 a	8.4 ± 0.02 b
pH KCl	4	4.4	0.01	7.8 ± 0.02 a	7.74 ± 0.02 b
Total Carbonates	4	11	<0.001	68.2 ± 0.4 a	71.4 ± 0.4 a
Total OM	4	20.5	<0.001	0.8 ± 0.02 a	1.63 ± 0.03 c
P ₂ O ₅ Olsen (mg/Kg Soil)	4	83.9	<0.001	34.8 ± 0.4 a	58.6 ± 0.4 d
K ₂ O (mg/Kg Soil)	4	28.3	<0.001	300.2 ± 4.6 a	313.6 ± 7.7 a
MgO (mg/Kg Soil)	4	99.8	<0.001	461.6±9.1ab	325 ± 4.1 c
CaO (mg/Kg Soil)	4	15.4	<0.001	11140±80.5a	10962±79.1a

Na ₂ O (mg/Kg Soil)	4	198.3	<0.001	21.8 ± 0.4 a	18 ± 0.8 a
N total (mg/Kg Soil)	4	52.5	<0.001	560 ± 4 a	1068.2±27.7c
Carbon (mg/Kg Soil)	4	20.5	<0.001	4.6 ± 0.1 a	9.5 ± 0.2 c
C:N ratio	4	4.7	0.008	8.3 ± 0.2 a	8.9 ± 0.4 a

Table 3. 2. Results of chemical soil analyses performed for in-situ degraded soils and in-situ reference soils in 2018.

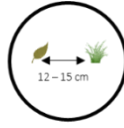
	Plant Species	Seed Tested #	Germinated Seeds #	Germination %
Neighboring Plants	<i>Aegilops triuncialis</i>	130	118	90.77
	<i>Echinops viscosus</i>	130	126	96.62
	<i>Eryngium creticum</i>	130	80	61.54
	<i>Hyoscyamus aureus</i>	130	125	96.15
Nurse Plants	<i>Trifolium subterraneum</i>	130	118	90.77
	<i>Melica inaequiglumis</i>	130	100	76.92

Table 3. 3. Seed germination percentages based on coleoptile emergence as a proxy of germination under controlled laboratory conditions during an 8 weeks period.

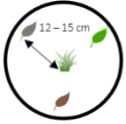
Illustrations



a. Nurse Plant (NP) alone : *Trifolium subterraneum* or *Melica inaequiglumis*



b. NP + Neighboring Community with 1 Plant (*Echinops viscosus*)



c. NP + Neighboring Community with 3 Neighbor Plants
(*Echinops viscosus*- *Hyoscyamus aureus*- *Aegilops triuncialis*)



d. NP + Neighboring Community with 4 Neighbor Plants
(*Echinops viscosus*- *Hyoscyamus aureus*- *Aegilops triuncialis*- *Eryngium creticum*)



e. Control: NP + 4 Neighboring plants of same species as NP
(*Trifolium subterraneum* X 4 or *Melica inaequiglumis* X 4)

Illustration 3. 1. Plant arrangements in pots.

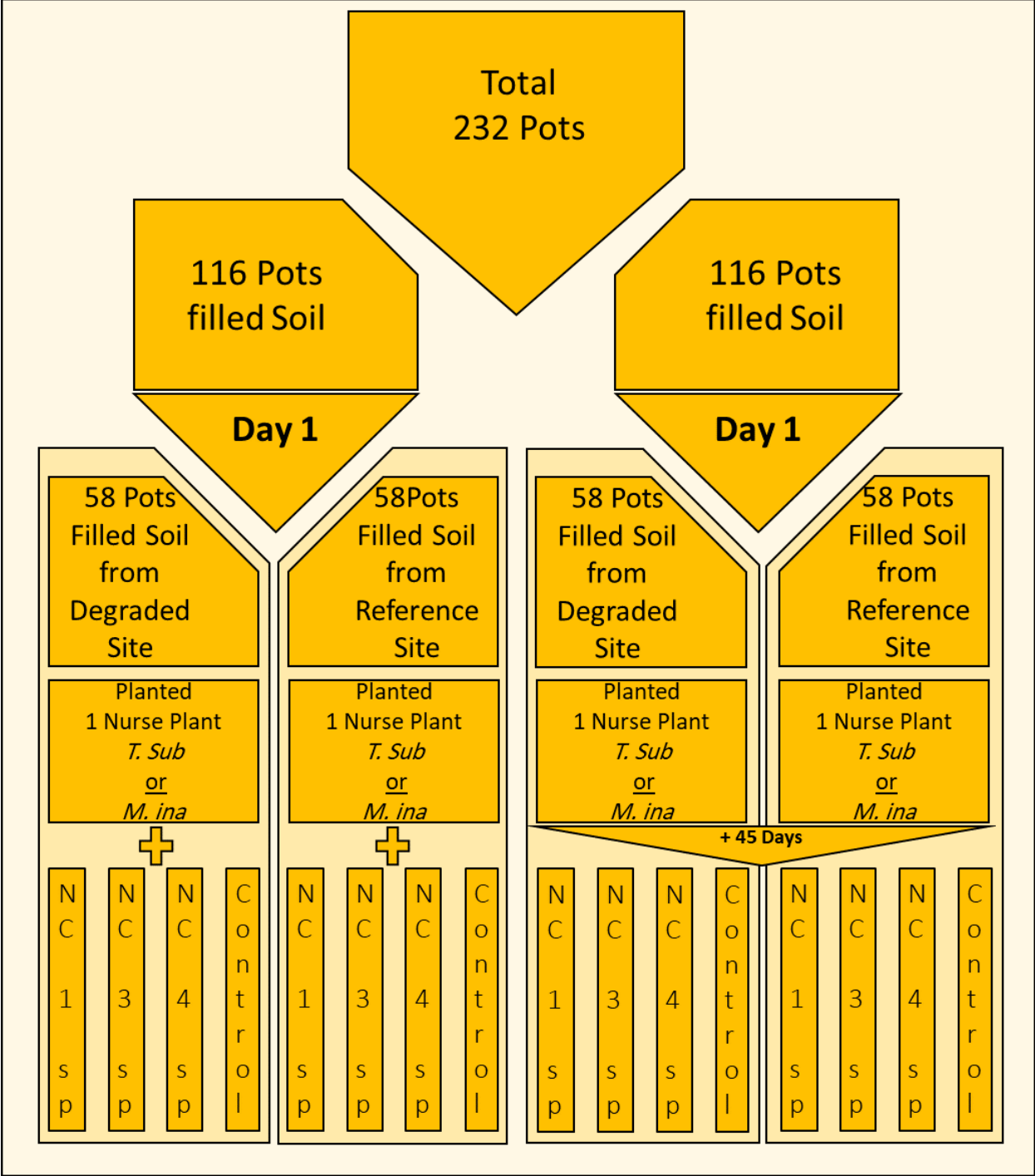


Illustration 3. 2. Schematic design for the experiment. Where *T. sub* is *Trifolium subterraneum*- *M. ina* is *Melica inaequiglumis*- NC is Neighboring Community with 1, 3, or 4 plants of different species/ pot.

DISCUSSION, CONCLUSION, AND PERSPECTIVES

The first objective of the thesis was to perform an extensive literature review regarding the different factors influencing the successes and failures of hydroseeding as a technique in the restoration of degraded semiarid Mediterranean environments (chapter 1). In view of this bibliographical review, we then considered an option of utilizing a cheaper and more natural based solution to aid in the restoration of such degraded environments, particularly the soil and herbaceous vegetation of degraded quarries- the use of 'Nurse Plants' (chapter 2). Those native plant species can potentially assist the establishment of introduced native plant species intended for quarry restoration. Finally, building on previous results, the effect of neighbors on two nurse plants was evaluated at varied plant complexities in different soil types (degraded quarry and surrounding reference ecosystem) and assessed when planted on the same or at separate dates (chapter 3).

Contribution toward a better understanding of quarrying status in Lebanon

Considered an important biodiversity hotspot, the Mediterranean Basin (Médail & Quézel, 1997) has been influenced by humans in some very intensive and extensive manner throughout the last 10,000 years, leading to 'anthropogenic' plant communities (Naveh & Kutiel, 1990), and resulting in extensively degraded areas (developed in the General Introduction section). Being located at the eastern end of the Mediterranean Basin, Lebanon, shares the same ecological woes; habitat fragmentations and losses, unsustainable exploitation of natural resources, pollution, invasive species, and climate change (MoE/UNEP/GEF, 2016) are all significant environmental stresses affecting the country (Section 1- Semiarid Mediterranean Environment Habitats). Unfortunately, from all previously cited ecological dire facing Lebanon, quarries are one of the most severe and pressing environmental issues (Section 1- Lebanon- a multi-challenging environment). With approximately 1,300 quarries causing extensive damage, destroying natural habitats, and changing landscape patterns (Khater et al., 2003). Regrettably, only a few quarries have undergone rehabilitation (MoE/UNDP/ECODIT, 2011). One such neglected quarry, located in the vicinity of Maqneh (a small village in the Beqaa plain near the Syrian border- refer to section 1, Quarries in Lebanon), was the one whose degraded soil and that of the surrounding reference grasslands soil, were used in the ex-situ experiments.

Contribution of the thesis to practical ecological restoration practices

Harsh dry summers followed by wet winters dictate a short growing season between the fall and spring periods of the year (Blondel & Aronson, 1999), rendering ecological restoration a challenging task in Mediterranean drylands (Cortina et al., 2011) (General Introduction- semiarid Mediterranean Environment Habitats). The work in this thesis revised the challenges facing hydroseeding practice in restoring semiarid Mediterranean environments, also assessing two plant species, a legume (*T. subterraneum* – Fabaceae) and a grass (*M. inaequiglumis*- Poaceae), as potential nurse plants to aid in restoring degraded quarries in a semiarid Mediterranean environment (chapters 1, 2, & 3).

Challenges facing hydroseeding practice in restoring semiarid Mediterranean environments

Using Hydroseeding as a restoration tool in a degraded Mediterranean environment (chapter 1) necessitates an in-depth understanding of several essential variables enabling one to overcome numerous obstacles. Those variable restrictions could be (I) biotic or (II) abiotic factors, further sub-categorized into (a) natural or (b) human-induced. In summary, (I-a) biotic natural-influenced factors such as weed competition and seed predation (grazing or pathogenic attacks); (I-b) biotic human-influenced factors involving the species in seed mixtures: Different types, percentage of various seeds, presence of native seeds, their morphological features, individual growth rates, and mycorrhizal inoculation. The abiotic factors were also further sub-divided into (II-a) abiotic natural-environmental factors related to site topography, aspect, edaphic characteristics, and water availability; and (II-b) abiotic human-influenced factors associated with the kind of aqueous solution utilized, the slurry component used, intervention season, watering, soil addition, and mulching.

Native species as potential ‘Nurse Plants’ used in restoring degraded quarries

This thesis permitted the assessment of two plant species, a legume (*T. subterraneum*– Fabaceae) and a grass (*M. inaequiglumis* – Poaceae), as potential nurse plants aiding in restoring a degraded quarry (chapters 2 & 3).

The studies, performed under ex-situ conditions, promoted more comprehension of plant-plant collaborations. Such interactions are associated with plant communities in semiarid

Mediterranean grasslands, with the possible use of native plants (from that same habitat) as nurse plants to aid in the rehabilitation of degraded systems. The outcome from this semi-controlled interspecific interaction experiment indicated that with both nurse plants, competition rather than facilitation dominated the interactions amongst the studied plant species, deduced thru measurements of different indicative traits. Nevertheless, it is possible to reason that such manipulations could yet be another step in the advancement of both fundamental and experimental research. When it comes to practical conservation and restoration processes, such results are also intriguing since they could provide diverse ways and means that might aid in detecting potential nurse plant species or structuring species capable of increasing the successional dynamics of a plant community. Although ex-situ studies cannot substitute in-situ experimentations (Forero et al., 2019), they could be the first step in selecting different designs, management methods, and various species needed to utilize in any ecological restoration procedure with less costly in-situ settings.

In-depth discussion of facilitation among plants, and the role of nurse plants.

Since the introduction of the plant-to-plant interaction concept in the early twentieth century, competition rather than facilitation, unfortunately, has been assumed to govern the interactions among plants in communities (chapter 2). This kind of interaction seems an obvious postulate since plants use those same limited and essential resources - that get even more restricted upon depletion. For decades, facilitation, as a concept, was mainly ignored and discarded from mainstream ecology until the last decade of the twentieth century, when its importance gradually increased. This new interest revealed numerous proofs that facilitation ameliorates the surrounding environments of other plants into more favorable ones. It also highlighted the momentous concept that facilitation escalates, in correlation, with increasing environmental stress, defined as any external factor or several factors that cause an individual or population to be less fit, diminishing its ability to regenerate biomass from energy. Those strains can be physical (direct effects of wind, waves, currents, etc.), physiological (droughts, temperatures, salinity, etc.), or even biotic in nature (predation, competition, disease, etc.). In literature, several microhabitat changes have been attributed to plants facilitating other plant species, either through direct positive mechanisms or indirect mechanisms. Direct mechanisms

involve modifications in soil, moisture, light, temperature, etc. Whereas indirect ones would entail incidental pollination, protection from herbivores, etc.

Facilitation, as a mechanism, has been noted to shift roles with competition amidst a shift in environmental stress. This alteration- termed Stress Gradient Hypothesis (General Introduction – ‘Nurse Plant’ concept as a restoration tool- Stress Gradient Hypothesis) - revolves around facilitation being prevalent in communities under high-stress factors, and on the contrary, it is less dominant in relatively benign conditions with less pressure thus, competitive interactions dominate. The SGH theory has been assessed under different factors, conditions, and habitats, amidst conflicting results, with some scientists applauding its validity while others criticized it (General Introduction – ‘Nurse Plant’ concept as a restoration tool- Stress Gradient Hypothesis- Critics of Stress Gradient Analysis).

A particular type of facilitation involving interactions between plants and various seedlings is the ‘Nurse Plant’ (General Introduction – ‘Nurse Plant’ concept as a restoration tool). It is the situation where mature plants have positive ‘nursing’ effects on seedlings, of the same or different species, under their canopy, compared to seedlings present outside their shelter. Theoretically, nursing mechanisms can affect varied stages of the beneficiary plants’ life, buffering and ameliorating non-optimal environmental situations (Bertness & Callaway, 1994). Its assistance can cross-thru seed trapping, seed sprouting, the sapling stage, moving through the different growth phases, and finally ending at reproduction. The literature cites tens of roles a nurse plant could achieve: rainfall capturing (Maestre et al., 2009), shade creation (thus decreasing soil water evaporation and dropping temperatures), frost-effect reduction, windbreaks (Lortie & Callaway, 2006), increasing seed trapping rates (Giladi et al., 2013), soil fertility enhancing (via litter accumulation) (Walker et al., 2001), predator protection (guarding seedlings against grazing, trampling, or reducing palatability) (Barbosa et al., 2009), and indirectly enhancing soil chemistry through mycorrhizal-colonization assistance.

How can the two tested nurse plants be employed in practical restoration practices?

Although results attained from the study, by calculating the RII, showed the prevalence of competition rather than facilitation among most plants. The initial results, especially with *Trifolium* forming compact swards (Gosling, 2005), revealing competition towards neighbor

plants, consequently, an inhibitory effect. The following year's results showed that incorporating the debris of *T. subterraneum* (chapter 2) into the soil will lead to a notable increase in organic matter (Gosling, 2005) significantly increasing total soil carbon and nitrogen. An increase in such essential elements will sequentially aid the re-establishment of soil fertility in degraded quarries. Another result worth highlighting is the facilitation of *T. subterraneum* as a *nurse plant* towards *T. subterraneum* as a *neighbor plant*, i.e., a pure stand of *T. subterraneum*. The outcome of such a combination can be profited from, as a soil restoring strategy, by establishing it the first year in a pure stand form as a foundation species (Coiffait-Gombault et al., 2012). This practice is highly desirable due to its several diverse and desirable qualities (dense, low spreading, annual plant, also being a legume). Later on, its dried biomass is mixed into the topsoil by small ungulates (goats or sheep) trampling. As a final step, during the next growing season, the seed mixture intended for restoration could be introduced.

As for the other tested nurse plant, *M. inaequiglumis*, the obtained results also revealed competition, from neighbor plants, rather than facilitation as a net outcome (chapter 3). Yet, a possible way to benefit from those results could be via capitalizing on the priority effect concept. Consequently, establishing *M. inaequiglumis*, unaccompanied, in degraded soils for a whole season, before introducing any seeds of species intended for restoration or any grazing strategy. Accordingly, capitalizing on its qualities being a perennial deciduous grass (thus, supplying the soil with ample OM in a short period), with an extensive hair-like root system (thus, knitting soil and reducing erosion), and ultimately regenerating the second season (accordingly, have the possibility of creating a favorable microclimate for newly germinating seedlings present in its vicinity), especially with an appropriate grazing regime.

Research perspectives

The fact that the obtained results of both nurse plants exhibited, in most situations, competition (at times in both directions) rather than facilitation towards neighbor plants does not reduce existing potentials in those two nurse plants as a natural restoration tool. Despite the protocol suggested by Gaudet and Keddy (1988, 1995) that aided in assessing whether facilitation or competition was present in an ex-situ setting (tested by the RII) is a simple yet very efficient and precise tool to evaluate the type of interaction present (Howard & Goldberg, 2001; Armas et al.,

2004; Liancourt et al., 2009). Some pioneers in the plant-facilitation field criticized the performance of such interactions in a greenhouse setting, claiming that studies of plant interactions in a greenhouse will almost always illustrate competition rather than facilitation. In a published book *'Positive Interactions and Interdependence in Plant Communities'* Callaway (2007) debated that “cramming several plants into a restricted area reduces their niche options, because conditions in greenhouses tend to be so benign that neighbors can have no real effects on the harsh conditions that exist in the real world”. He backs up his arguments by stating examples like steady water supply, protection from winds as buffers, high atmospheric humidity, and high moisture effects in the vicinity of leaves. All those factors present in a greenhouse setting might lead to stress reduction, conclusively rendering facilitation less likely. Callaway concluded that without the presence of real-life stress situations, any performed study is notably less possible to deliver facilitation (Callaway, 2007).

Repetition of the same experiments in an in-situ setting- the quarry

To verify whether the preceding arguments are credible similar experiments could be implemented, but in a quarry setting instead (in-situ). Initially, several of the overpowering variables mentioned in Chapter 2 (grazing, pedestrian circulation, site securing, and permits...) must be addressed. In theory, the experiment could be repeated in the same manner (chapter 2 - Material and Methods) but with some minor technical modifications suitable for an in-situ setting. Those modifications could consider the following: (1) Replacing tray-seed sowing and transplanting with direct on-site seeding at proper timing, in a fenced protected location, at the degraded quarry site, (2) Initiation of the experiment towards November, to rely on rain-fed watering, rather than the supplied irrigation water in the greenhouse, (3) Prior to the initiation of the second phase of the experiment, some ungulates to be shortly introduced to graze and trample the area.

Implementing the results of the ex-situ experiments in an in-situ setting

To capitalize on the results of the experiments, summarized as follows: *T. subterraneum* could be planted in an in-situ setting as a pure stand in the first year, followed in the second year by the seed mixture intended for restoration. The following experiments with different objectives could be undertaken, in an in-situ setting (quarry), (1) Assess total OM, nitrogen, & C levels pre-and post-application. (2) Testing the efficiency of *T. subterraneum*, as a nurse plant, in providing control, for example, towards erosion (due to its dense ground-hugging nature), shade, wind, or cold protection. (3) Testing quantity, density, and influence of voluntarily emerging *T. subterraneum* saplings in the second year (being a geocarpic plant) as potential nurse plants. (4) Testing best grazing practices regarding *T. subterraneum* with respect to time, intensity, and type.

As for *M. inaequiglumis*, the experimenting with it within an in-situ setting, by capitalizing on the fact of being a perennial grass. Consequently, its use as a nurse plant for restoration practices can be further investigated in an in-situ setting based on the following qualities: (1) being a perennial hence, examination of its nursing effect on saplings in the vicinity. Additionally, being a caespitose rhizomatous, with dense clump characteristics qualifies it as a nurse plant with capabilities of trapping wind or water drifted seeds, amassing water, creating shade, ... (2) The evaluation of *M. inaequiglumis* potentials (with its deep, extensive, and well-spread fibrous root system) for erosion control, especially in newly degraded areas. (3) Assessing the aspect of having a growing season commencing in fall, benefiting from natural rainfall and early growth and establishment initiation, with its effect on spring germinating seedlings.

Effect of inoculation of *Trifolium subterraneum* seeds with *Rhizobium* sp.

In the course of both experiments, and especially during the early establishment phase, some *T. subterraneum* seedlings (about 5-7% of the total number) failed to develop and grow, retaining weak yellow postures. Being a legume with nitrogen-fixing capabilities (Ferreira & Castro, 2005), *T. subterraneum* could form a symbiotic relationship with the bacteria *Rhizobium leguminosarum* var *trifolii* (Sanford et al., 1994). Unfortunately, visual roots examination of the lagging saplings exposed a lack of Rhizobial nodules. Thus, a possible follow-up on the issue in a future experiment could include an experimental design with inoculation (or without) of *T.*

subterraneum (as nurse plants designated for restoration) with Rhizobium sp. Hypothetically, those inoculated plants should establish faster, set added vegetative growth, enrich the soil with nitrogen, and ultimately benefit the intended target plants.

Testing the priority effect principal

In the course of the second experiment, the concept of priority effect was tested by spacing the planting date between the nurse and the neighbor plants by a 45 days interval. Results (Refer to the Discussion section in Chapter 3) indicated the presence (though weak) of a priority effect. This concept could be experimented upon further through different scenarios: (1) Creating various planting times between the tested nurse and neighbor plants to experiment priority effect concept. (2) Testing this concept within an in-situ setting (directly in the quarry), where the tested nurse plant could be introduced earlier, and later introduce intended target plants.

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