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How species colonize gaps after soil disturbance in temporary ponds? Implication of species traits

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Abstract

This work aims to review the existing theoretical literature and experiments on plant species colonising gaps after soil disturbance. It attempts to evaluate the various mechanisms by which plants regenerate among the soil openings within the Mediterranean temporary ponds. Intensity and frequency of disturbances are key factors in the response of communities. Knowing the specificity of plant strategies and the species assembly process is important for a better understanding of the impact of soil disturbance on the structure of temporary ponds community, and their mechanisms of resilience. Under the scope of these mechanisms, we will assess the contribution of seed bank by regrowth of buried seeds, vegetative propagules growth via clonal propagation and dispersion of propagules. Soil disturbance has a biotic effect on competition giving a chance to competitively inferior species.

Key words: *dispersion, propagules, resilience, seeds, soil disturbances, temporary ponds*

INTRODUCTION

Temporary ponds are described as small size wetlands appearing without flow depressions, they are filled with water during the winter and dried out during the summer. Very common under Mediterranean climate, temporary ponds, host a high and unique fauna and flora that contribute to regional [ANGELIBERT *et al.* 2006; WILLIAMS *et al.* 2003], and global freshwater biodiversity [OERTLI *et al.* 2009], the fact that they include many rare and threatened species [KEDDY 2010], gives them an important role and value in the landscape [ZACHARIAS *et al.* 2007]. However facing an increased number of disturbances, temporary ponds are easily overlooked and vulnerable to threats [CANCELA DA FONSECA *et al.* 2008]. The growth of research activity focusing upon ponds has risen significantly over the past few years, therefore the acquaintance with plant communities' strategies, related to temporary ponds is not well known, especially the role of plant species life traits, however their flora is

a key factor for biodiversity conservation [OERTLI *et al.* 2009].

The aim of this work is to review the theories and experiments related to community responses in relation to mechanical soil disturbance and life traits contribution of species involved in the colonisation of the generated gaps. Several experimental studies have tested the effect of soil disturbance on the biodiversity in different ecosystems [KALAMEES, ZOBEL 2002; KOTANEN 1996; MAYER *et al.* 2004; MÜLLER *et al.* 2014; PAKEMAN, SMALL 2005; ROGERS, HARTNETT 2001; SEBASTIA, PUIG 2008; ZOBEL *et al.* 2000]. A small proportion of these were carried out in Mediterranean temporary ponds [DEVICTOR *et al.* 2007; SAHIB *et al.* 2011]. There is still a lack of reviews highlighting life history traits of plant species involved in the colonisation of temporary gaps that have opened in wetlands. Furthermore, there are no published reviews related to post recolonization mechanisms in temporary ponds after soil disturbance.

COMMUNITY RESPONSES

Community's responses to mechanical disturbance depend both on the potential of the ecosystem itself and the native community. Three mechanisms (vegetative multiplication, seed stock expression, seeds dispersion) have a proportional role in the post disturbance reconstitution, controlled by the external conditions of the environment (in temporary ponds it is mainly hydrology regime and submersion duration). Two main parameters describe the structural relationship of a community: species richness and species interaction. These two parameters refer to the species biodiversity and the complexity of the interactions within community. However, the intensity and frequency of disturbances are decisive factors in the response of communities as explained by HUSTON [1994] in a two-dimensional model. He establishes a close relationship between the species richness, resilience and the frequency of disturbances. An intermediate frequency of perturbation will produce a maximum level of richness. Supporting CONNELL'S [1978] theory of intermediate disturbance hypothesis with a maximum level of biodiversity, as a consequence of an intermediate regime of disturbance, consequently it's assumed to maintain biodiversity at high level by creating gaps for the new germinations of inferior competitive species, allowing them to newly appear in the community [DEVICTOR *et al.* 2007; MÜLLER *et al.* 2014], allowing this way disturbance to be a component of plant dynamic [PICKETT, CADENASSO 2005] by generating in one hand over time a development of multiple and stochastic successions, fluctuating around an average value, but only after elimination of the pre-existing vegetation and on other hand generating continuum model by successional age [PRACH *et al.* 2014]. Temporary ponds are facing three possible scenarios related to the change of disturbance magnitude; the resilience process (intermediate magnitude of soil disturbance) allows the input of propagules in the temporary ponds without interference magnitude the statement change (high magnitude) interferes with recruitment and reduces species richness. The resistance (low magnitude) allows competition to eliminate less competitive species with no recruitment of new seeds. The example taken from Mediterranean temporary ponds in Morocco [RHAZI *et al.* 2012] shows that the ponds located in an intermediate magnitude of disturbed soil's environment (forest lands) houses a greater richness in characteristic and rare species, than those located in high magnitude of soil disturbance (agricultural lands). Disturbance had a significant influence on species richness, increases specifically the pond's characteristic and rare species but not in the richness of opportunistic. However, a few annuals did show a greater richness in agricultural ponds (*Eryngium atlanticum* Batt. & Pit., *Lythrum tribracteatum* Salzm ex Sprengel, *Verbena supina* L.) [FENNANE *et al.* 1999; 2007] related to their specific traits (e.g. production of many

seeds), making them more tolerant to disturbances. Richness, of annual species, reacts positively to soil disturbance, reflecting their general affinity according to their life traits.

An increase of the magnitude of disturbance is firstly attached to the complete destruction of biomass [GRIME 1979] and secondly by the decrease of the probability of individuals' survival, the shortening of the life cycle and the increase of investment in reproduction mechanisms are two adaptive responses to the decrease which are induced by the rise of the magnitude in disturbances [ERIKSSON 1997; PAUSAS *et al.* 2004]. Moreover, it also leads to individual's mortality depending on their size [BROSE *et al.* 2017]. In this case, the adaptive response is the conversion of allocation in breeding a large number of small seeds rather than a small number of large seeds. The multiplication of seeds disperses the risk of extinction of the population in order to overcome the low probability of survival of individuals [MOLES, WESTOBY 2004]. The relative stability of the communities expresses their resistance, and it is evaluated by measuring the variables of state that might be: a) distinctive of the ecosystem; b) measurable and/or computable; c) and must have an ecological importance (e.g. richness, density, biomass, recovery).

SPECIES STRATEGIES TO FULFFIL GAPS

The most common models that include species strategies.

- The r-K strategy [MCARTHUR, WILSON 1967] adopted by many authors in the 'competition-colonization compromise' [GERITZ *et al.* 1999; JAKOBSSON *et al.* 2006; KISDI, GERITZ 2003; TILMAN 2004]. Which is the association of two main strategies of recruitment among gaps: 'r' type strategy: when species promote reproduction (e.g. high reproductive rates, rapid growth, early sexual maturity, short life cycle, many small size seeds with high dispersion). This type of species, predominate in frequently disturbed environments and have a low capacity for competition. 'K' type strategy where species invest in maintaining the individual (e.g. few large size seeds with copious reserves [JAKOBSSON, ERIKSSON 2003], slow growth, long life cycle, late sexual maturity). Species with a 'K' strategy are favoured by low disturbance environments and are high competitors.
- The 'CDS' strategy C-Competitive, D-disturbed, S-Stressed model developed by MURPHY *et al.* [1990]: which is more related to aquatic environments, applying and analysing the models on the temporary ponds lead us to the results below.

SEXUAL REPRODUCTION 'r' TYPE STRATEGY

Within temporary ponds, under disturbance and during stress conditions enforced by the fluctuation of

hydrology regime, seeds contribute to conserve populations more than the plant itself. The creation of a sustainable stock of viable seeds in the soil is a strategy used by species to be potentially and permanently present in the community and intervene in post disturbance regeneration [ZABINSKI *et al.* 2000]. This regeneration occurs when conditions became favourable to germination, eased forward by the high density of seed bank rate because any low-density may limit recruitment [PAKEMAN, SMALL 2005].

The composition of the seed stock depends on the relative longevity of each species seeds type [PAKEMAN, SMALL 2005], as well as the seeds input rates (e.g. seeds production) and the seeds exit rates (e.g. germination, death, migration to deeper horizons) plus the differential allocation of resources to sexual reproduction, the size and number of seeds produced, and life history traits that leads to large composition differences between species in seed stock.

In accordance with pioneering studies carried out in temporary ponds [DEIL 2005; GRILLAS *et al.* 2004; MEDAIL *et al.* 1998; ZEDLER 1987] and as predicted by MCARTHUR and WILSON's [1967] theory, temporary ponds community shows a predominance of r-strategy species which attribute to a faster recovery, and accordingly a high resilience of the ecosystem. The richness of 'r' type strategy, species especially annuals respond positively to soil disturbance. This reflects the general affinity of those plants to disturbance according to their life trait.

The experiments by VAN DER VALK, DAVIS [1978], DEVICTOR *et al.* [2007], and SAHIB *et al.* [2009; 2011] carried out show distinctly that seed banks 'and spores' contributed strongly to temporary ponds restoration, once annuals are dominant among the plants. Generally, the species with the highest density in the seed bank (*Juncus pygmaeus* Rich. ex Thuill., *Ranunculus baudotii* Godr., *Glyceria fluitans* (L.) R.Br., and *Isoetes fluitans* M.I. Romero) are also the most abundant in the established vegetation. However, soil disturbance affects significantly the vertical distribution of seeds stock. The turning over of the soil brings back the seeds to the surface (upper layers). Which the deep, maintain their germination capacity.

SAHIB *et al.* [2011] found that in post disturbance regeneration, the seed bank contributed strongly in plant resilience. Their availability and high abundance among the temporary ponds facilitated the post disturbance recruitment. Authors found that soil disturbance leads to a slight decrease in seed density in the upper layers of sediment, reflected in a decrease in the germination success and establishment of seedling due to their burial (mostly small sized ones). DEVICTOR *et al.* [2007] show a spatial and temporal storage effect of soil disturbance. Large part of the seed bank is stored in deep soil layers. The seeds are not abolished but buried for a certain period. Furthermore, soil disturbance forces relatively large proportion of rare and endangered species living in temporary ponds to

form long-term persistent seed bank. This is the case of the semi aquatic *Damasonium alisma* Mill., shown in the same study. After soil disturbance *Damasonium alisma* Mill. seeds were more abundant and had a better germination rate coming from deeper soil layers. Soil disturbance had not only accumulated most of the seeds in deep layers, but also concentrated the best seeds. The burial of seeds maintained their germination capacity. *Damasonium alisma* Mill. dormant seeds remain this way as long as they are constantly damped or constantly submerged. Nevertheless, SAHIB *et al.* [2011] and DEVICTOR *et al.* [2007] found that a set of conditions needs to be fulfilled in order to achieve a successful post disturbance recruitment in temporary ponds, particularly the hydrology regime, pointed out to be a major factor that filters seedling recruitment [SAHIB *et al.* 2009; VAN DER VALK, DAVIS 1978].

VEGETATION REPRODUCTION 'k' TYPE STRATEGY

Soil disturbance alters the storage organs generally responsible for high biomass production [FAHRIG *et al.* 1994; WINKLER, FISCHER 2001], it leads to a significant reduction in biomass, particularly of perennials as a direct effect but it does not reduce their richness [MÜLLER *et al.* 2014; SAHIB *et al.* 2011]. Most perennials tolerate soil disturbance, thus sexual reproduction is highly important for the resilience of the newly created gaps.

Vegetative reproduction is the detachment of vegetative organs from the parent plant [KLIMES *et al.* 1997]. An individual can complete its own cycle from specific organs such as bulbs, rhizomes, and stolons [FISCHER, VAN KLEUNEN 2002; PENNING, CALLAWAY 2000]. The clonal aspect is important because each perennial is able to produce many new plants in relatively short time.

The experience built in experimental disturbed plots by SAHIB *et al.* [2011] demonstrates a rapid regeneration within the community since the first post disturbance year, it suggests a strong effect of lateral colonization from undisturbed neighbouring areas, by the geophytes (e.g. *Isoetes fluitans* M.I. Romero, *Narcissus viridiflorus* Schousb). Furthermore, their corms played an important role in recolonization, as they were probably barely affected by the disturbances. The vegetative organs of *Bolboschoenus maritimus* (L.) Palla and *Eleocharis palustris* (L.) Roem. & Schult. allow rapid recolonization as well. Even some bulbs of *Bolboschoenus maritimus* (L.) Palla, remained unaffected, the physical split awakens the dormant buds on the bulbs and compensates for any negative effects of disturbance for an additional regeneration.

In addition, though disturbance can cause local extinction of perennials, it could be compensated by lateral colonisation from adjacent areas. The peripheral colonisation effect was mentioned by AMAMI

et al. [2009]. The first established species were the clonal perennials *Bolboschoenus maritimus* (L.) Palla and *Eleocharis palustris* (L.) Roem. & Schult. They colonised vegetatively by means of rhizomes and runners, the species were present in the neighbouring vegetation and colonised the experimental disturbed plots via a border effect. Another example taken from the ponds in the Netherland by VAN WIJK, TROMPENAARS [1985] showed that for the aquatic *Potamogeton trichoides* Cham & Schldtl. the maintenance of the population seems to depend almost completely on the turions, since the germinated seeds were not found. The complete dependence of this macrophyte on vegetative reproduction is a warning sign on the invasive ability of some aquatic macrophytes using this reproduction strategy, giving the ability to spread promptly.

The vegetative reproduction gives species multiple benefits: new individuals can settle more easily through physiological integration, or through the transfer of resources between descendants, especially in stressed environments [AMIAUD *et al.* 2000; ERIKSSON 1997; VAN KLEUNEN *et al.* 2001]. Vegetative reproduction may have the main role in the conservation of the species among sites, while that sexual reproduction may have the main role in the colonization of new sites.

DISPERSION

Dispersion enables the colonisation process in new gaps, the same as the propagule's ability to initiate and expand successfully in new areas. In local scale, vegetative propagules play a part. Yet in amphibious or aquatic plants, vegetative propagules have greater potential than seeds for long distance dispersal within a stressed environment [CHARPENTIER *et al.* 2000] while seeds are generally suitable for long distance dispersion [BARETT *et al.* 1993]. Seeds durability is moderated by variable abiotic and biotic conditions before and after dispersion [LONG *et al.* 2014]

Temporary ponds communities work as meta-communities [DE MEESTER *et al.* 2005], where direct and indirect dispersal mechanisms (e.g. wind, water, birds and even animals), play a great role in the biotic connection [VANSCHOENWINKEL *et al.* 2008a, b] moreover, a weaker dispersion can lead to a decline of the number of ponds [OERTLI *et al.* 2005].

AMAMI *et al.* [2009] used experimental plots with sterilised soil of temporary ponds. The study showed that the nearest and the relatively most abundant species quickly become established in the sterilised plots such as *Glyceria fluitans* (L.) R.Br., *Pulicaria Arabica* (L.) Cass., *Lolium rigidum* Gaud., *Plantago coronopus* L. The greater abundance of these species in experimental sterilised plots comes from their efficient dispersal, which could be associated with the small size of the seeds and also with the presence of a dispersal structure (pappus). Whilst dispersion of the bulbous perennial *Scilla autumnalis* L. was low,

which produces few large seeds and has a poor capacity for dispersal by seeds and almost none by vegetative spread, others, such as *Alisma spp.* and *Mentha spp.*, have lacunae tissues filled with air (seeds pericarp), that allows them a good ability to disperse.

Dispersion is a random process that has more chance to occur during the dry period in temporary ponds. Seeds, spores and propagules have a great likelihood to reach gaps when ponds are dried. However, many aquatic species have special mechanisms such the ability to float before they are fixed, and this is the case of the helophyte *Juncus spp.* While *Glyceria sp.*, *Eleocharis sp.*, *Scirpus sp.* have achenes that remain enclosed by air within one or more associated bracts, and therefore float until they become waterlogged [SCULTHORPE 1967; STANFORTH, CAVERS 1976].

Water birds frequenting temporary ponds are also a mean of dispersion: the seeds of *Glyceria fluitans* (L.) R.Br., *Alisma plantago-aquatica* L., and the vegetative fragments of *Myriophyllum sp.* were contained in the mud carried on the feet of birds [COOK 1990]. It should be pointed out that spores' origin (sexual process or not) is unimportant to the dispersion of plants [COOK 1988], the main aim is that newly created gaps might be colonised depending on the ability of propagules to establish themselves and root successfully in these new gaps.

COMPETITION

SOIL DISTURBANCE AND COMPETITION

Disturbance consists of the mechanisms which limit the plant biomass by causing its partial or complete destruction [GRIME 2001]. It reduces mainly the biomass of higher competitors and opens habitat for the weaker ones (mostly endemic, threatened and rarest species). These weak competitive species must deal with intraspecific competition, which is the first post germination obstacle to face within the newly created gaps. Moreover, these endemic and rare species are sensitive to disturbance; they are considered biotic indicators to assess the ecological integrity within temporary ponds [VAN DEN BROECK *et al.* 2015]. In wetlands GAUGET and KEDDY [1988] demonstrated that the weaker competitors are shaded by the higher ones (macrophytes), and showed that the competitive ability comes from the biomass produced aboveground this increases the exclusive potential, the connection between the productivity and the intensity of competition is close [TOWLAN-STRUT, KEDDY 1996]. In temporary ponds, competition is a biotic threat for rare and endemic species [RHAZI *et al.* 2009] (e.g. the clonal plant species *Bolboschoenus maritimus* (L.) Palla and a rare quillwort *Isoetes setacea* Lam.).

The experimental removal of perennials via soil disturbance by DEVICTOR *et al.* [2007] lowered the competition and enhanced the viability of *Damasonium alisma* Mill. (a typical ephemeral threatened

wetland). The creation of gaps lowers the biomass productivity, which is important for the weak competitors. On the contrary, the dominance of high competitors leads to the closing of ecosystems and to the exclusion of some ecosystems components such as bryophytes of temporary ponds, which occurs only for a very short time when subjected to competition [HUGONNOT 2011]. However, a positive effect was noticed on bryophyte richness in grasslands, due to the soil disturbance's short-term interspecific and intraspecific low competition at newly created gaps [MÜLLER *et al.* 2014].

In temporary ponds, flooding (elevation and duration) limits the extension of high competitors. Nonetheless, flood tolerant species expand at the edges and shallow parts [YU *et al.* 2012]. Competitors progression in and around temporary ponds can be managed by soil disturbance, because clonal progression leads to a decrease of solar radiations and temperature that interrupt the growth of weaker competitors.

BROSE and TIELBORGER [2005] showed that the removal of higher competitors as well as the extent of flooding have similar consequences on plant community structure among temporary ponds mainly on the amphibious species. The competition by dominant species is an important factor settling annual communities with the addition of the location according to hydrology gradient competition decreases with increasing hydrological stress [HOUGH-SNEE *et al.* 2014].

STRESS AND SPECIES COMPETITIVENESS

It is currently recognized that stress and disturbance reduce the intensity of competitive interaction. The importance of competition is inversely proportional to stress or disturbance [GRIME 1973; HUSTON 1979]. Stressful conditions change the faculty of species, whilst in normal conditions competition is determinant in species germination. According to TILMAN [1982] the intensity of competition changes along the environmental gradient.

The establishment of species in temporary ponds is mainly driven by hydrology regime fluctuation. The growth of plants is potentially limited by the annual cycle fluctuation of drought and flooding, been considered the main characteristic of the life cycle of temporary ponds during the year [BONIS 1993]. The length of hydroperiod affects strongly the regional richness, intermediate hydroperiod intermediate levels of dry down may maintain high regional diversity among wetlands [ZOKAN, DRAKE 2015]. Temporary wetlands plant community is dominated by annuals, which escaped the favourable conditions during flooding as seed bank, besides annuals being proved genetically conditioned by the water high and strictly dependent on previous rainfall conditions, soil moisture and water storage capacity [MINEA, IOANA-TOROIMAC 2016] In these communities, the intensity of competition may depend on the stress alongside the

topographic gradient (i.e. edge and centre of temporary ponds).

An experimental combination of added seeds (to simulate artificially the competition) to disturbed soil and fluctuated hydrology, carried out by [SAHIB *et al.* 2009] shows a biomass production due to hydrology regime firstly (65% of variance explained) and by mechanical soil disturbance secondly (23% of variance explained). The results obtained in this study confirm that, in Mediterranean temporary ponds, hydrology is the major factor that structures and selects the species of the community, it modifies any disturbance effects, and it influences the impact of competition's intensity on primary production. The experiment showed that competition has a role in structuring the communities only when the conditions for production are favourable (saturation of the sediment by water). Flooding conditions in the Mediterranean region are transitory and their duration varies considerably from year to year, which reduce its long-term impact. Thus, the effect of local soil disturbance on the vegetation and its richness (especially during the plants growing season), can be modulated by the regional environmental variables. AMAMI *et al.* [2009] confirmed this result: in temporary ponds, plants development is controlled by the environmental filter of hydrological regime, followed by the species traits. The climate is considered to exert a large-scale disturbance, which is overlapped to the local-scale one.

Under a Mediterranean climate, the major abiotic constraints were found to be the frequency of droughts or the occurrence of dry periods during the plant growth [ANGELER, MORENO 2007; REY, AL-CANTARA 2000]. These constraints define the selection of species and hence the composition of the post disturbance communities. BREWER *et al.* [1997] and LENSSEN *et al.* [1999] confirmed these findings in wetlands: according to the authors, competition for itself plays an important role in the less flooded parts of wetland habitats. Conversely, in case of flooding, the community's production remains low, closely linked to the trade-off between growth and soil resources acquisition and the effective conservation of resources under flooding conditions [HOUGH-SNEE 2014]. Consequently, the competition remains limited and does not affect the species richness. These results put forward that in favourable hydrological conditions (wetter soil), the variable rates of species' successful reproduction in Mediterranean temporary ponds affect only the richness of communities. Accordingly, environmental conditions are a better predictor of post disturbance competition strategies.

Furthermore, within the temporary ponds peripheral zones, competition by the dominant terrestrial species is more important, whereas flooding limits their growth at the centre zone of the ponds, even when competition is lacking. Those results were obtained by BUDELSKY and GALATOWITSCH [2000] and BROSE and TIELBORGER [2005], who investigated respectively the response of perennial sedges to flooding and

competition in Australian temporary wetlands, and the inter-specific competition among the annual plant community in agricultural grassland in Germany.

Competition is the biotic factor that manages species richness at the peripheral zone of the temporary ponds, where abiotic stress is much lower than in the central zone. The competition's intensity ranges from negative to positive along the topographic gradient from the centre to the periphery within temporary ponds [PRACH *et al.* 2014; WATERKEYN *et al.* 2008].

As mentioned before, temporary ponds species escape the hostile conditions buried as seeds, the model of species distribution is most likely mediated by an interaction of hydrology duration, which is restricting the susceptibility of habitat even in the case of soil disturbance.

CONCLUSIONS

Soil disturbance is a set of overlapping factors that can have either positive or negative effects on the conservation of temporary ponds species. It can lead to a decrease in species cover (i.e. biomass), and consequently favours weaker competitor's growth. However, when soil disturbance is more frequent, the community size decreases. Gaps creation and heterogeneity within temporary ponds can maintain the structure and dynamic of plants community. To be rapid and resilient, plants developed a strategy thanks to the high seed banks inputs. Temporary ponds have a good resistance related to the ability of their functional groups to generate in a post perturbation state. They are able to compensate those that have been affected by the disturbance [SCHROLL *et al.* 2009].

Meanwhile, reproduction, dispersion and competition for establishment are the most important strategies developed by species in temporary ponds and involved in the post disturbance colonisation process. Seeds germination and vegetative propagules is another important step in the reproduction cycle of the plants. Species dynamic allocation under environmental conditions is decisive to realize new gaps, responses to these conditions give an overview about species potential to establish in post disturbance gaps. Process and implications are mainly related to species competitiveness within communities and filters persistence. The strategies afterward seem to be valuable to predict and outline the role of soil disturbance to select species traits and strategies. However, other factors such as hydrology are considered stressful. In fact, it plays a key role in the selection of species and can interact with soil disturbance effect or hide any biotic interaction (e.g. competition).

REFERENCES

AMAMI B., RHAZI L., RHAZI M., BOUAHIM S., GRILLAS P. 2009. Vegetation recolonisation of a Mediterranean temporary pool in Morocco following small-scale experimental disturbance. *Hydrobiologia*. Vol. 634. Iss. 1 p. 65–76.

AMIAUD A., BONIS A., BOUZILLE J.B. 2000. Conditions de germination et rôle des herbivores dans la dispersion et le recrutement d'une espèce clonale: *Juncus gerardi* Lois [Germination conditions and the role of herbivores in dispersal and recruitment of a clonal species: *Juncus gerardi* Lois]. *Canadian Journal of Botany*. Vol. 89. No. 1 p. 1430–1439.

ANGELER D.G., MORENO J.M. 2007. Zooplankton community resilience after press-type anthropogenic stress in temporary ponds. *Ecological Applications*. Vol. 17. Iss. 4 p. 1105–1115.

ANGÉLIBERT S., INDERMUEHLE N., LUCHIER D., OERTLI B., PERFETTA J. 2006. Where hides the aquatic biodiversity in the Canton of Geneva (Switzerland)? *Archives des Sciences*. Vol. 59 p. 225–234.

BARRETT S.C.H., ECKERT C.G., HUSBAND B.C. 1993. Evolutionary processes in aquatic plants populations. *Aquatic Botany*. Vol. 44. Iss. 2–3 p. 105–145.

BONIS A. 1993. Dynamique des communautés et mécanismes de coexistence des populations de macrophytes immergées en marais temporaires [Dynamics of communities and coexistence mechanisms of macrophyte populations immersed in temporary ponds]. PhD Thesis. Université de Montpellier II pp. 173.

BREWER J.S., LEVIN J.M., BERTNESS M.D. 1997. Effects of biomass removal and elevation on species richness in a New England salt marsh. *Oikos*. Vol. 80. No. 2 p. 333–341.

BROSE U., BLANCHARD J.L., EKLOF A., GALIANA N., HARTVIG M., HIRT MR., KALINKAT G., NORDSTROM M.C., O'GORMAN E.J., BJORN C.R., SCHNEIDER F.D., THEBAULT E., UTE J. 2017. Predicting the consequences of species loss using size-structured biodiversity approaches. *Biological Reviews*. Vol. 92. Iss. 2 p. 684–697.

BROSE U., TIELBORGER K. 2005. Subtle differences in environmental stress along a flooding gradient affect the importance of inter-specific competition in an annual plant community. *Plant Ecology*. Vol. 178. Iss. 1 p. 51–59.

BUDELSKY R.A., GALATOWITSCH S.M. 2000. Effects of water regime and competition on the establishment of a native sedge in restored wetlands. *Journal of Applied Ecology*. Vol. 37. Iss. 6 p. 971–985.

CANCELA DA FONSECA L., CRISTO M., MACHADO M., SALA J., REIS J., ALCAZAR R., BEJA P. 2008. Mediterranean temporary ponds in Southern Portugal: Key faunal groups as management tools? *Pan-American Journal of Aquatic Science*. Vol. 3. Iss. 3 p. 304–320.

CHARPENTIER A., GRILLAS P., THOMPSON J.D. 2000. The effect of population size limitation on fecundity in mosaic populations of clonal macrophyte *Bolboschenus maritimus* (Cyperaceae). *American Journal of Botany*. Vol. 87. Iss. 4 p. 502–507.

CONNELL J.H. 1978. Diversity in tropical rain forests and coral reefs. *Science*. Vol. 199. Iss. 4335 p. 1302–1310.

COOK C.D.K. 1988. Wind pollination in aquatic angiosperms. *Annals of Missouri Botanical Garden*. Vol. 75. No. 3 p. 768–777.

COOK C.D.K. 1990. *Aquatic plant book*. The Hague, The Netherlands. SPB Academic Publishing. ISBN 9051030436 pp. 228.

DE MEESTER L., DECLERCK S., STOCKS R., LOUETTE G., VAN DE MEUTTER F., DE BIE T., MICHELS E., BRENDONCK L. 2005. Ponds and pools as model systems in conservation biology, ecology and evolutionary biology. *Aquatic Conservation*. Vol. 15. Iss. 5 p. 715–725.

- DEIL U. 2005. A review on habitats, plant traits and vegetation of ephemeral wetlands – A global perspective. *Phytocoenologia*. Vol. 35. No. 2–3 p. 533–705.
- DEVICTOR V., MORET J., MACHON N. 2007. Impact of ploughing on soil seed bank dynamics in temporary pools. *Plant Ecology*. Vol. 192. Iss. 1 p. 45–53.
- ERIKSSON O. 1997. Clonal life histories and the evolution of seed recruitment. In: *The ecology and evolution of clonal plants*. Eds. H. de Kroon, J. M. van Groenendael. Leiden, The Netherlands. Backhuys Publishers p. 211–226.
- FAHRIG L., COFFIN D.P., LAUENROTH W.K. 1994. The advantage of long-distance clonal spreading in highly disturbed habitats. *Evolutionary Ecology*. Vol. 8. Iss. 2 p. 172–187.
- FENNANE M., IBN TATTOU M., MATHEZ J., OUYAHYA A., EL OUALIDI J. 1999. *Flore pratique du Maroc [Practical flora of Morocco]*. Travaux de l'Institut Scientifique. 1ère série Botanique 36. Rabat, Morocco. ISBN 2366610009 pp. 560.
- FENNANE M., IBN TATTOU M., OUYAHYA A., EL OUALIDI J. 2007. *Flore pratique du Maroc [Practical flora of Morocco]*. Travaux de l'Institut Scientifique. 2ème série Botanique 38. Rabat, Morocco. ISBN 2366600003 pp. 636.
- FISCHER M., VAN KLEUNEN M. 2002. On the evolution of clonal plant life histories. *Evolutionary Ecology*. Vol. 15. Iss. 4–6 p. 565–582.
- GAUDET C.L., KEDDY P.A. 1988. A comparative approach to predicting competitive ability from plant traits. *Nature*. No. 334 p. 242–243.
- GERITZ S.A.H., VAN DER MEIJDEN E., METZ J.A.J. 1999. Evolutionary dynamics of seed size and seedling competitive ability. *Theoretical Population Biology*. Vol. 55. Iss. 3 p. 324–343.
- GRILLAS P., GAUTHIER P., YAVERCOVSKI N., PERENNOU C. 2004. Mediterranean temporary pools: (1). Issues relating to conservation. Functioning and management. *Tour du Valat*. Arles. ISBN 2-9103-6849-1 pp. 120.
- GRIME J.P. 1973. Competitive exclusion in herbaceous vegetation. *Nature*. Vol. 242 p. 344–347.
- GRIME J.P. 1979. *Plant strategies and vegetation processes*. Chichester. John Wiley & Sons. Ltd. ISBN0471996920 pp. 222.
- GRIME J.P. 2001. *Plant strategies, vegetation processes, and ecosystem properties*. Chichester. John Wiley & Sons. Ltd. ISBN 978-0-470-85040-4 pp. 456.
- HOUGH-SNEE N., NACKLE L.L., SOO-HYUNG K., KERN E. 2014. Does plant performance under stress explain divergent life history strategies? The effects of flooding and nutrient stress on two wetland sedges. *Aquatic Botany*. Vol. 120. P. B p. 151–159.
- HUGONNOT V. 2011. Les bryophytes et les bryocénoses du site d'Entraygues (Var, France) comme outil d'évaluation d'un projet de renaturation hydrologique [Bryophytes and bryocenoses at the Entraygues site (Var, France) as an evaluation tool for a hydrological renaturation project]. *Ecologia mediterranea*. Spec. iss. Vol. 37. Iss. 2 p. 45–56.
- HUSTON M. 1979. A general hypothesis of species diversity. *American Naturalist*. Vol. 113. No. 1 p. 81–101.
- HUSTON M. 1994. *Biological diversity. The coexistence of species of changing landscapes*. Cambridge University Press. Cambridge, UK. ISBN 0521369304 pp. 681.
- JAKOBSSON A., ERIKSSON G. 2003. Trade-offs between dispersal and competitive ability: a comparative study of wind-dispersed Asteraceae forbs. *Evolutionary Ecology*. Vol. 17. Iss. 3 p. 233–246.
- JAKOBSSON A., ERIKSSON G., BRUUN H.H. 2006. Local seed rain and seed bank in a species-rich grassland: Effects of plant abundance and seed size. *Canadian Journal of Botany*. Vol. 84. Iss. 12 p. 1870–1881.
- KALAMEES R., ZOBEL M. 2002. The role of the seed bank in gap regeneration in a calcareous grassland community. *Ecology*. Vol. 83. Iss. 4 p. 1017–1025.
- KEDDY P.A. 2010. *Wetland ecology: Principles and conservation*. Cambridge University Press. New York. ISBN 0521739675 pp. 497.
- KISDI E., GERITZ S.A.H. 2003. On the coexistence of perennial plants by the competition-colonization trade-off. *American Naturalist*. Vol. 161. No. 2 p. 350–354.
- KLIMES L., KLIMESOVA J., HENDRIKS R., VAN GROENENDAEL J.M. 1997. Clonal plant architecture: A comparative analysis of form and function. In: *The ecology and evolution of clonal plants*. Eds. H. De Kroon, J.M. van Groenendael. Leiden. The Netherlands. Backhuys Publishers p. 1–29.
- KOTANEN P.M. 1996. Revegetation following soil disturbance in a California meadow: The role of propagule supply. *Oecologia*. Vol. 108. Iss. 4 p. 652–662.
- LENSSSEN J.P.M., MENTING F.B.J.W., VAN DER PUTTEN H., BLOM C.W.P.M. 1999. Control of plant species richness and zonation of functional groups along a freshwater flooding gradient. *Oikos*. Vol. 86. No. 3 p. 523–534.
- LONG R. L., GORECKI M. J., RENTON M., SCOTT J.K., COLVILLE L., GOGGIN D.C., COMMANDER L.E., WESTCOTT D.A., CHERRY H., FINCH-SAVAGE W.E. 2014. The ecophysiology of seed persistence: A mechanistic view of the journey to germination or demise. *Biological Reviews*. Vol. 90. Iss. 1 p. 31–59.
- MAYER P., ABS C., FISCHER A. 2004. Colonisation by vascular plants after soil disturbance in the Bavarian Forest – Key factors and relevance for forest dynamics. *Forest Ecology and Management*. Vol. 188 p. 279–289.
- MCARTHUR R.H., WILSON E.O. 1967. *The theory of island biogeography*. Princeton University. Press. ISBN 9781400881376 pp. 203.
- MEDAIL F., MICHAUD H., MOLINA J., PARADIS G., LOISEL R. 1998. Conservation de la flore et de la végétation des mares temporaires dulçaquicoles et oligotrophes de France méditerranéenne [Conservation of the flora and vegetation of the temporary freshwater and oligotrophic pools of Mediterranean France]. *Ecologia Mediterranea*. Vol. 24. Iss. 2 p. 119–134.
- MINEA G., IOANA-TOROIMAC G. 2016. Land use impact on overland flow: micro-scale field experimental analysis. *Journal of Water and Land Development*. No. 29 p. 67–74. DOI 10.1515/jwld-2016-0013.
- MOLES A.T., WESTOBY M. 2004. Seedling survival and seed size: A synthesis of the literature. *Journal of Ecology*. Vol. 92. Iss. 3 p. 372–383.
- MURPHY K.J., RØRSLETT B., SPRINGUEL I. 1990. Strategy analysis of submerged lake acrophyte communities: an international example. *Aquatic Botany*. Vol. 36. Iss. 4 p. 303–323.
- MÜLLER J., HEINZE J., JOSHI J., BOCH S., KLAUS V.H., FISCHER M., PRATI D. 2014. Influence of experimental soil disturbances on the diversity of plants in agricultural grasslands. *Journal of Plant Ecology*. Vol. 7. Iss. 6 p. 509–517.
- OERTLI B., BIGGS J., CEREGHINO R., GRILLAS P., JOLY P., LACHAVANNE J. 2005. Conservation and monitoring of temporary wetland biodiversity: Introduction. *Aquatic*

- Conservation Marine and Freshwater Ecosystems. Vol. 15. Iss. 6 p. 535–540.
- OERTLI B., CÉRÉGHINO R., HULL A., MIRACLE R. 2009. Pond conservation: from science to practice. *Hydrobiologia*. Vol. 634. Iss. 1 p. 1–9.
- PAKEMAN R., SMALL J.L.J. 2005. The role of the seed bank, seed rain and the time of disturbance in gap regeneration. *Journal of Vegetation Science*. Vol. 16. Iss. 1. p. 121–130.
- PAUSAS J.G., BRADSTOCK R.A., KEITH D.A., KEELEY J.E.C.A. 2004. Plant functional traits in relation to fire in crown-fire ecosystems. *Ecology*. Vol. 85. Iss. 4 p. 1085–1100.
- PENNINGS S.C., CALLAWAY R.M. 2000. The advantages of clonal integration under different ecological conditions: A community-wide test. *Ecology*. Vol. 81. Iss. 3 p. 709–716.
- PICKETT S.T.A., CADENASSO M.L. 2005. Vegetation succession. In: *Vegetation ecology*. Ed. E. van der Maarel. New York. Blackwell Publishing. p. 172–198.
- PRACH K., ŘEHOUNKOVÁ K., LENCOVÁ K., JÍROVÁ A., KONVALINKOVÁ P., MUDRÁK O., STUDENT V., VANĚČEK Z., TICHÝ L., PETŘÍK P., ŠMILAUER P., PYŠEK P. 2014. Vegetation succession in restoration of disturbed sites in Central Europe: The direction of succession and species richness across 19 seres. *Applied Vegetation Science*. Vol. 17. Iss. 2 p. 193–200.
- REY P., ALCANTARA J.M. 2000. Recruitment dynamics of a fleshy-fruited plant (*Olea europea*), connecting patterns of seed dispersal to seedling establishment. *Journal of Ecology*. Vol. 88. Iss. 4 p. 622–633.
- RHAZI L., GRILLAS P., RHAZI M., AZNAR J.C. 2009. Ten-year dynamics of vegetation in a Mediterranean temporary pool in western Morocco. *Hydrobiologia*. Vol. 634. Iss. 1 p. 185–194.
- RHAZI L., GRILLAS P., SABER E., RHAZI M., BRENDONCK L., WATERKEYN A. 2012. Vegetation of Mediterranean temporary ponds: A fading jewel? *Hydrobiologia*. Vol. 689. Iss. 1 p. 23–36.
- ROGERS W.E., HARTNETT D.C. 2001. Temporal vegetation dynamics and recolonization mechanisms on different sized soil disturbances in tallgrass prairie. *American Journal of Botany*. Vol. 88. Iss. 9 p. 1634–1642.
- SAHIB N., RHAZI L., GRILLAS P. 2011. Post-disturbance dynamics of plants communities in a Mediterranean temporary pool (western Morocco). *Botany*. Vol. 89. No. 2 p. 105–118.
- SAHIB N., RHAZI L., RHAZI M., GRILLAS P. 2009. Experimental study of the effect of hydrology and mechanical soil disturbance on plant communities in Mediterranean temporary pools in Western Morocco. *Hydrobiologia*. Vol. 634. Iss. 1 p. 77–86.
- SCHROLL H., THORN P., KJÆRGÅRD B. 2009. Resilience is more than an elastic jump. *Journal of Transdisciplinary Environmental Studies*. Vol. 8. No. 1 p. 1–2.
- SCULTHORPE C.D. 1967. *The biology of aquatic vascular plants*. London. UK. Edward Arnold Ltd. ISBN 3874292576 pp. 610.
- SEBASTIA M., PUIG T.L. 2008. Complex vegetation responses to soil disturbances in mountain grassland. *Plant Ecology*. Vol. 199. Iss. 77 p. 3007–3013.
- STANFORTH R.J., CAVERS P.B. 1976. An experimental study of water dispersal in *Polygonum* spp. *Canadian Journal of Botany*. Vol. 54. No. 22 p. 2587–2596.
- TILMAN D. 1982. *Resource competition and community structure*. Princeton. New Jersey. USA. Princeton University Press. ISBN 9780691083025 pp. 296.
- TILMAN D. 2004. Niche tradeoffs, neutrality, and community structure: A stochastic theory of resource competition, invasion, and community assembly. *Proceedings of the National Academy of Sciences (U.S.A.)*. Vol. 101. Iss. 30 p. 10854–1086.
- TWOLAN-STRUTT L., KEDDY P.A. 1996. Above and below-ground competition intensity in two contrasting wetland plant communities. *Ecology*. Vol. 77. Iss. 1 p. 259–270.
- VAN DEN BROECK M., WATERKEYN A., RHAZI L., GRILLAS P., BRENDONCK L. 2015. Assessing the ecological integrity of endorheic wetlands with focus on Mediterranean temporary ponds. *Ecological Indicators*. Vol. 54 p. 1–11.
- VAN DER VALK A.G., DAVIS C.B. 1978. The role of seed banks in the vegetation dynamics of prairie glacial marshes. *Ecology*. Vol. 59. Iss. 2 p. 322–335.
- VAN KLEUNEN M., FISCHER M., SCHMID B. 2001. Effects of intraspecific competition on size variation and reproductive allocation in a clonal plant. *Oikos*. Vol. 94. Iss. 3 p. 515–524.
- VAN WIJK R.J., TROMPENAARS H.J.A.J. 1985. On the germination of turions and the life cycle of *Potamogeton trichoides* Chain. et Schld. *Aquatic Botany*. Vol. 22. Iss. 2 p. 165–172.
- VANSCHOENWINKEL B., GIELEN S., SEAMAN M., BRENDONCK L. 2008a. Any way the wind blows – Frequent wind dispersal drives species sorting in ephemeral aquatic communities. *Oikos*. Vol. 117. Iss. 1 p. 125–134.
- VANSCHOENWINKEL B., WATERKEYN A., VANDECAETSBECK T., PINEAU O., GRILLAS P., BRENDONCK L. 2008b. Dispersal of freshwater invertebrates by large terrestrial mammals: A case study with wild boar (*Sus scrofa*) in Mediterranean wetland. *Freshwater Biology*. Vol. 53. Iss. 11 p. 2264–2273.
- WATERKEYN A., GRILLAS P., VANSCHOENWINKEL B., BRENDONCK L. 2008. Invertebrate community patterns in Mediterranean temporary wetlands along hydroperiod and salinity gradients. *Freshwater Biology*. Vol. 53. Iss. 9 p. 1808–1822.
- WILLIAMS P., WHITFIELD M., BIGGS J., BRAY S., FOX G., NICOLET P., SEAR D. 2003. Comparative biodiversity of rivers, streams, ditches and ponds in an agricultural landscape in Southern England. *Biological Conservation*. Vol. 115. Iss. 2 p. 329–341.
- WINKLER E., FISCHER M. 2001. The role of vegetative spread and seed dispersal for optimal life histories of clonal plants: A simulation study. *Evolutionary Ecology*. Vol. 15 p. 281–301.
- YU J., WANG X., NING K., LI Y., WU H., FU Y., ZHOU D., GUAN B., LIN Q. 2012. Effects of salinity and water depth on germination of *Phragmites australis* in coastal wetland of the Yellow River delta. *Clean – Soil, Air, Water*. Vol. 40. Iss. 10 p. 1154–1158.
- ZABINSKI C., WOJTOWICZ T., COLE D. 2000. The effects of recreation disturbance on subalpine seed banks in the northern Rocky Mountains. *Canadian Journal of Botany*. Vol. 78. No. 5 p. 577–582.
- ZACHARIAS I., DIMITRIOU E., DEKKER A., DORSMAN E. 2007. Overview of temporary ponds in the Mediterranean region: Threats, management and conservation issues. *Journal of Environmental Biology*. Vol. 28. Iss. 1 p. 1–9.
- ZEDLER P.H. 1987. *The ecology of Southern California vernal pools: A community profile*. U.S. Fish and Wildlife Service Biological Report. Vol. 85 p. 7–11.
- ZOBEL M., OTSUS M., LIIRA J., MOORA M., MÖLS T. 2000. Is small-scale species richness limited by seed availability or microsite availability? *Ecology*. Vol. 81. Iss. 12 p. 3274–3282.

ZOKAN M., DRAKE J.M. 2015. The effect of hydroperiod and predation on the diversity of temporary pond zooplankton communities. Ecology and Evolution. Vol. 5. No. 15

p. 3066–3074.

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W jaki sposób gatunki kolonizują puste miejsca w okresowych stawach po uszkodzeniach gleby? Wpływ cech gatunkowych

STRESZCZENIE

Przedstawiona praca miała na celu przegląd teoretycznych i eksperymentalnych badań nad gatunkami roślin, które kolonizują puste miejsca pozostałe po uszkodzeniach gleby. Podjęto próbę oceny różnych mechanizmów, które prowadzą do regeneracji roślinności w lukach powstających w okresowych stawach rejonu Morza Śródziemnego. Intensywność i częstość uszkodzeń są kluczowymi czynnikami w odniesieniu do reakcji zespołów roślinnych. Znajomość specyfiki strategii roślin i procesów tworzenia zespołów ma znaczenie dla lepszego zrozumienia wpływu uszkodzeń gleby na strukturę zespołów i ich mechanizmy odpornościowe. W ramach tych mechanizmów oceniono udział banku nasion poprzez kiełkowanie zachowanych nasion, rolę propagul (diaspor) wegetatywnych przez rozmnażanie klonalne i dyspersję propagul. Uszkodzenia gleby stwarzają szansę gatunkom o słabszym potencjale konkurencyjnym.

Słowa kluczowe: *dyspersja, nasiona, odporność, propagule, stawy okresowe, uszkodzenia gleby*