DOI: 10.2478/jwld-2018-0050

JOURNAL OF WATER AND LAND DEVELOPMENT
2018, No. 38 (VII–IX): 137–145
PL ISSN 1429–7426, e-ISSN 2083-4535

Available (PDF): http://www.itp.edu.pl/wydawnictwo/journal; http://www.degruyter.com/view/j/jwld

Received 09.11.2017
Reviewed 05.03.2018
Accepted 12.04.2018

A – study design
B – data collection
C – statistical analysis
D – data interpretation
E – manuscript preparation
F – literature search

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

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For citation: Sahib N. 2018. How species colonize gaps after soil disturbance in temporary ponds? Implication of species traits. Journal of Water and Land Development. No. 38 p. 137–145. DOI: 10.2478/jwld-2018-0050.

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 (law 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; PENNINGS, 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 & Schltdl. 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 metacommunities [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; STANIFORTH, 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 gabs might be colonised depending on the ability of propagules to establish themselves and root successfully in these new gabs.

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 *Isoëtes 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, ALCANTARA 2000]. Theses 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).

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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*