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PERSPECTIVE

Factors of global change affecting plants act at different levels of the ecological hierarchy

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SUMMARY

Plants and ecosystems worldwide are exposed to a wide range of chemical, physical, and biological factors of global change, many of which act concurrently. As bringing order to the array of factors is required in order to generate an enhanced understanding of simultaneous impacts, classification schemes have been developed. One such classification scheme is dedicated to capturing the different targets of global change factors along the ecological hierarchy. We build on this pioneering work, and refine the conceptual framework in several ways, focusing on plants and terrestrial systems: (i) we more strictly define the target level of the hierarchy, such that every factor typically has just one target level, and not many; (ii) we include effects above the level of the community, that is, there are effects also at the ecosystem scale that cannot be reduced to any level below this; (iii) we introduce the level of the landscape to capture certain land use change effects while abandoning the level below the individual. We discuss how effects can propagate along the levels of the ecological hierarchy, upwards and downwards, presenting opportunities for explaining non-additivity of effects of multiple factors. We hope that this updated conceptual framework will help inform the next generation of plant-focused global change experiments, specifically aimed at non-additivity of effects at the confluence of many factors.

Keywords: multiple factors, ecological hierarchy, global change, non-additivity, ecosystem, community.

INTRODUCTION

Ecosystems and plants worldwide are affected by a wide range of environmental conditions, including factors of human-caused global environmental change (Sage, 2020). These global change factors tend to not occur in isolation but rather appear together (Bowler et al., 2020; Côté et al., 2016; Gunderson et al., 2016; Jackson et al., 2021; Paine et al., 1998), making the systematic study of the simultaneous impacts of a large number of factors/stressors a necessity (Orr et al., 2020). Owing to several reasons, including logistics, and more fundamentally, the combinatorial explosion problem (that is, the number of treatment combinations rapidly increasing with the number of factors considered), experimental work on such multiple impacts on plants is not very common. Experimental work on soil has shown that an increasing number of factors (from zero to ten) causes progressively worsening effects on soil processes and biodiversity (Rillig et al., 2019). This study employed a combinatorial design, using random draws from a pool of factors to generate an experimental gradient in factor number, de-emphasizing factor identity, and composition. Very similar effects have also been found for plants, exemplified by experimental work on Arabidopsis (Zandalinas, Fritschi, et al., 2021; Zandalinas, Sengupta, et al., 2021), tomato (Pascual et al., 2023), soybean (Peláez-Vico et al., 2023), rice and maize (Sinha et al., 2022), and also for plant communities experimentally exposed to up to six factors of global change (Speißer et al., 2022). More recently, a global observational study has also found the signature of a number of factors in the biodiversity and ecosystem function data encompassing over 200 different ecosystems (Rillig et al., 2023). These studies collectively highlight the frequent co-occurrence of factors, that joint effects of many factors leave a signature on plants, soils, and ecosystems, and that a renewed research focus on studying the effects of numerous concurrently acting factors is of great importance.

An important step toward making sense of the wide range and diversity of factors is to classify them according to first principles because this places the divergent set of stressors in a common framework and context. Such a classification has recently been accomplished for a broad set of 30 factors/stressors with abstract plant/ soil systems at the local scale in mind (Rillig, Ryo, et al., 2021). Beyond the usefulness of such a classification in devising new research questions about the diversity and divergence of factors, and in science communication, this exercise also revealed the potential utility of using this information for predicting experimental results (Rillig, Ryo, et al., 2021). Subsequently, a comprehensive analysis of classification approaches for stressors/factors, following the systematic 5W1H approach of information gathering (5W1H: what, when, where, who, why, and how), offered additional modes by which global change factors can be arranged and understood in terms of their similarity (Orr et al., 2022).

Classification approaches also need to explicitly take into account that stressors may manifest themselves at different levels of the ecological hierarchy (Orr et al., 2022). This perspective was not included in the earlier classification approach (Rillig, Ryo, et al., 2021), but was introduced in a seminal paper (Simmons et al., 2021) that distinguished the action of different factors of environmental change along the ecological hierarchy. We here build on this analysis, focusing explicitly on plants as focal organisms, and considering a different configuration of ecological hierarchies that also explicitly includes the landscape level.

Our overall goal is to use such organizational principles for global change factors to offer a path toward better understanding the effects of an increasingly diverse suite of these drivers on terrestrial ecosystems, and in particular on plants.

FACTORS OF GLOBAL CHANGE ENTERING AT DIFFERENT LEVELS OF THE ECOLOGICAL HIERARCHY

The traditional view of stressor effects (exemplified in ecotoxicology) assumes that such factors affect organisms at the cellular/biochemical level and that effects then propagate up along the ecological hierarchy (de Souza Machado, Wood, et al., 2019). While this is true for many factors, clearly this is not the case for all. Examining a broad range of factors affecting plants and terrestrial ecosystems, it becomes apparent that indeed by far most factors unfold their proximate effect at the level of the individual plant (Table 1); that is, they affect physiology, biochemistry, or cellular processes in plants. They could for example be resources, abiotic factors, or toxins (Rillig, Ryo, et al., 2021). Accordingly, measurements taken at this level capture such responses, including biomass, and physiological and stress responses. It seems clear that by far most experimental studies on plants address this level as well (Felton & Smith, 2017). This is because this is the *de facto* targeted level, and because of ease of experimentation compared to other levels in the hierarchy. Any such effects can then propagate up the level of the hierarchy, unless there are buffering effects and compensatory mechanisms that prevent this from happening (Connell & Ghedini, 2015).

However, there are also other factors at play that enter into the ecological hierarchy above the level of the individual (Simmons et al., 2021), including population, community, ecosystem, and landscape (Table 1). What we mean by that, is that these other factors exert their

Table 1 Global change factors (examples) and the different levels of the ecological hierarchy at which their effects manifest, as well as the plant-related parameters that are typically measured at each level

Global change factor (examples)	Ecological level at which factor manifests	Response variables (or indicators) typically measured
Habitat fragmentation; changes to landscape-level configuration of ecosystems	Landscape/ Macrosystems (regions)	Connectivity; configuration of landscape elements; dispersal
Habitat conversion (for example from grassland to urban garden or agricultural field), degradation; fire (stand-replacing); Microplastic (physical effects)	Ecosystem	Primary production; nutrient and energy fluxes; ecosystem structure
Invasive plants	Community (assemblage, food web)	Competitive or facilitative interactions; community composition and diversity
Overharvesting (e.g. clearcutting, or use of medicinal or ornamental plants)	Population	Population size and spatial structure; also: evolutionary responses
Elevated atmospheric CO_2; N deposition; warming; drought; flooding; artificial light at night (ALAN); UV-radiation; salinity; heavy metals; pesticides; microplastic (chemical effects); nanoplastic; per- and polyfluorated alkyl substances (PFAs) and other classes of organic chemical pollutants	Individual	Biomass; physiological responses; molecular/ biochemical responses; toxic effect relationships (dose–response)

proximate impacts by definition at these levels above the individual and that how they enter into this hierarchy cannot be reduced to the level(s) below.

For example, the factor habitat fragmentation only appears at the level of the landscape or region, which we introduce into our scheme of hierarchies for this purpose, as it makes no sense to apply it to levels below, since what is being fragmented is a landscape or region; for example by building a road in a rainforest. Similarly, habitat conversion or degradation occurs at the scale of ecosystems, such as for example the removal and replacement of all vegetation in the context of urbanization, or the conversion of a forest to agricultural land. In this case, the entire system is being re-engineered, and this effect cannot be understood to act directly at a level above or below the ecosystem. A special case is certain pollutants like microplastic, which by means of being particles, can affect direct physical changes to the soil (de Souza Machado, Lau, et al., 2019), thus directly affecting an ecosystem property (soil structure). Likewise, invasive plants are by definition an addition to the species pool, and thus directly pertain to the level of community (Simmons et al., 2021). At the level of population, factors that directly affect the number of individuals takes shape, such as local overharvesting of plants.

There are some key differences to the scheme offered before (Simmons et al., 2021). First, we here focus on plants and terrestrial systems. Second, we only identify one target level for each factor, following the definition of factor action defined above, whereas in the previous any global change factor was conceptualized as affecting many different levels in the ecology hierarchy. There may be few exceptions, like flooding will primarily directly affect the individual plant, but if a large-scale flood occurs it could impact dispersal or fragment habitats, thus entering at the landscape scale. Third, we here include factors whose effects manifest at the level of the ecosystem (and above) directly, which was not included in the previous conceptual model, where impacts of global change drivers stopped at the level of the community. Finally, we add the level of the landscape to accommodate land use change effects that play out at this scale, while merging the levels of ‘metabolism/ physiology’ and ‘individual’.

The above classification organized by ‘level of entry’ of a factor of course does not imply that the factor or stressor does not have ripple-on effects at level(s) above or below it. Quite the opposite is the case, for example, habitat fragmentation can very much affect community composition (through changes in dispersal limitation), eventually even trickling down to affecting populations and individual organisms. Likewise, changes that affect individuals can propagate up to affect populations (given effects on reproduction or mortality), communities (as governed by species interactions), and potentially also ecosystem process rates, as mediated by functional similarity (Eisenhauer et al., 2023). Using the example of climate extremes, this upward effect propagation from the level of plant individuals to the ecosystem has been discussed previously (Felton & Smith, 2017). It is thus important to emphasize that in the proposed ordering system we are not speaking about final effects, but about proximate levels at which a factor is acting or for which it is defined in the first place. Effect propagation in both directions—upward and downward (see Figure 1)—will mean that effects converge at certain levels, where they can contribute to non-additive overall effects.

The classification also makes no assumption about the scale of occurrence of a factor or stressor: while all factors discussed here are global in scope, they may be more local or regional in occurrence and severity, such as nitrogen deposition (Vitousek, 1994). As a regionally occurring factor, nitrogen deposition affects plants at the level of the individual, since it is a resource. And elevated atmospheric CO_2, a factor that is very much global in distribution and occurrence, as an atmospheric factor relatively well-mixed, unfolds its proximate effects also at the level of individual plants, since CO_2 is a resource for plants.

THE WAY FORWARD

We believe embracing our scheme helps understand multi-factor impacts on plants for several reasons. At the most basic level, it is important to realize the distribution of factors acting at different levels of the ecological hierarchy, since just studying responses at the individual level will miss several key drivers whose effects manifest above this level, at the population, community, ecosystem or landscape. We see four main points on which to focus in future research.

(i) *Understanding non-additivity of effects*—The fact that different factors not only differ in a variety of mechanisms of action, traits, and organismal targets (Orr et al., 2022) but that they also enter into the ecological hierarchy at different levels, means that this is a potential additional source of non-additivity of effects (Figure 1) to consider and explore (Simmons et al., 2021), beyond synergistic or antagonistic effects that occur at the scale of the individual plant (Rillig, Lehmann, et al., 2021). Identifying the mechanisms underpinning such effect non-additivity should be a major research focus.

(ii) *Adjusting the scope of experiments*—Factors that enter above the level of the individual are logistically much more challenging to study and thus there is likely less experimental evidence for effects, and increasingly studies will tend to shift to observational approaches, since experiments at the landscape level are logistically challenging or impossible. However, it will be increasingly important to design ambitious experiments that explicitly take into account the different entry points of

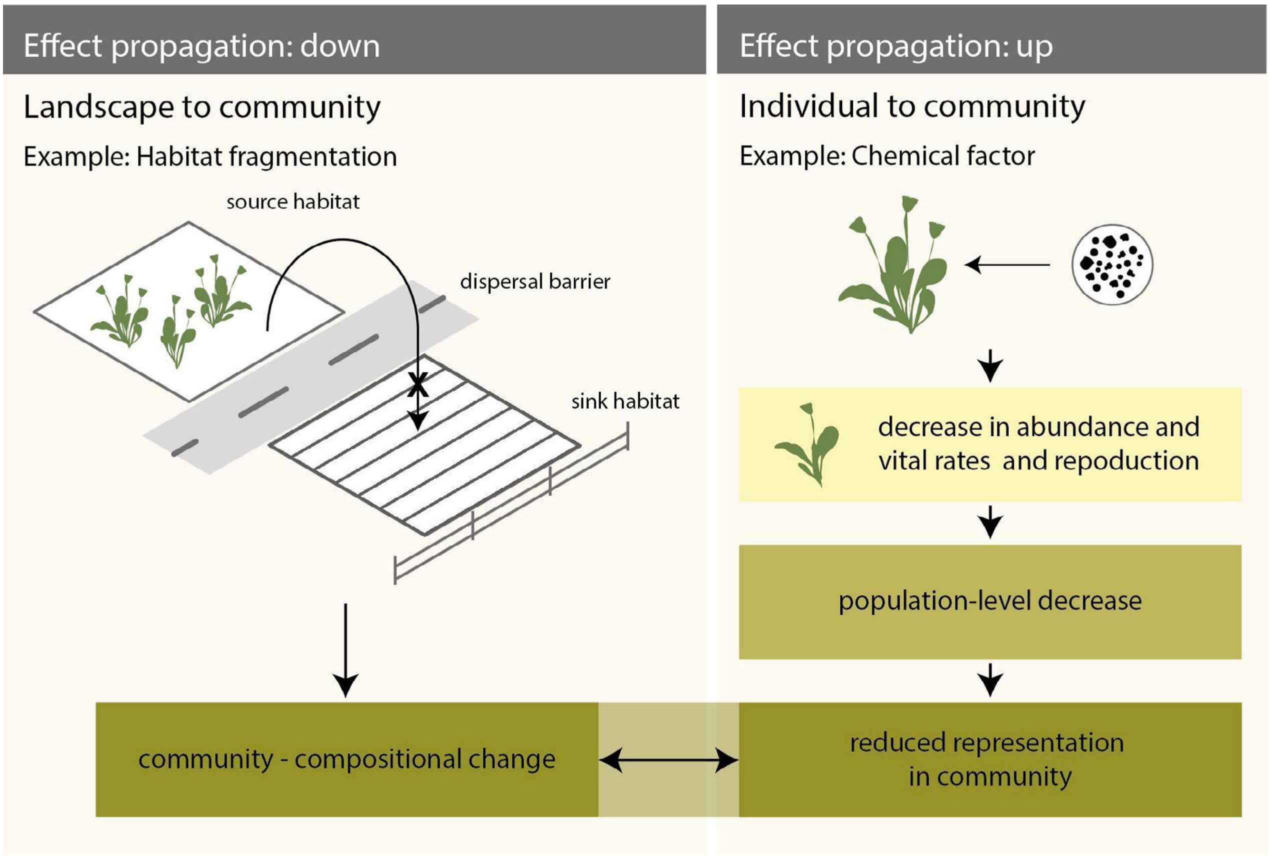

Figure 1. Effect propagation (downward and upward) is an important feature to consider in a framework that explicitly considers effects materializing at different levels of the ecological hierarchy. On the left, landscape level effects (factor: habitat fragmentation, in this case creating of a dispersal barrier) lead to a plant species A (or its key symbiont, such as a pollinator) no longer reaching a certain habitat. Within this habitat, due to this landscape-level reconfiguration, the target plant species will disappear, leading to community compositional change. On the right side, effects propagate up from the level of the individual to the community, via changes in population. In this case, a chemical pollutant negatively affects plants of species B, causing changes in vital rates and growth; these translate to population-level changes and eventually, the relative abundance of this plant species B will decrease in the target community. In these two examples, effects converge at the level of the community, where they can interact, for example, plant species A could have been lost from the community due to habitat fragmentation, and perhaps this was a main competitor of plant species B affected by chemical pollution.

effects and their propagation. Useful tools for achieving this will be innovative mesocosm experiments (coupled with process models); an example of an approach at the ‘landscape’ scale is the ‘Metatron’, an experimental infrastructure that includes 48 connected habitat patches (Legrand et al., 2012).

(iii) *Identifying sources of resilience*—Across the different levels of the ecological hierarchy, researchers will by necessity assess different response variables (Simmons et al., 2021). The fact that different parameters are measured means that responses cannot be directly compared in terms of effects and their attenuation across the different levels of the ecological hierarchy. For example, in terms of multi-factor impacts on plants, at the individual level, researchers will measure plant growth, survival, and physiological responses (Zandalinas, Sengupta, et al., 2021), but at the level of the plant community the focus by necessity shifts to primary production and community composition (Speißer et al., 2022). Effects at different levels of the same driver could be compared by using effect size estimates; this way, attenuation or exacerbation across the different levels could be assessed. This will permit improved understanding of effect propagation across the different levels and will allow us to identify sources of resilience to external drivers residing at the different levels (Thorogood et al., 2023).

(iv) *Detecting the first emergence of effects*—Signals of global change may first emerge at levels other than the one at which they primarily act, depending on at which level of the hierarchy the signal of global change emerges from the noise (Gamelon et al., 2023). Work on birds has shown that this emergence can happen at a higher level than that of the primary level (Gamelon et al., 2023): in this case, for climate change, the signal was first apparent at the level of the population, not at the level of the individual (traits, vital rates), where this factor primarily acts. It is unclear if this type of effect emergence can happen more broadly for other factors of global change, their interaction, and specifically, also for plants.

CONCLUSIONS

Plants in various different contexts (including agriculture, urban, and natural ecosystems) are exposed to a multitude of factors of global change, and we need to embrace this reality in the next generation of global change experiments. Adopting this view of multiple concurrent drivers acting on plants necessitates an appreciation of several of these global change drivers manifesting at the level above the individual plant, generating additional potential sources of non-additivity of effects, and facilitating thinking about resilience residing at different levels of the hierarchy.

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CONFLICT OF INTEREST

The authors have no conflicts of interest to declare.

REFERENCES

Bowler, D.E., **Bjorkman, A.D.**, **Dornelas, M.**, **Myers-Smith, I.H.**, **Navarro, L.M.**, **Niamir, A.** ***et al.*** (2020) Mapping human pressures on biodiversity across the planet uncovers anthropogenic threat complexes. *People and Nature*, **2**, 380–394.

Connell, S.D. & **Ghedini, G.** (2015) Resisting regime-shifts: the stabilising effect of compensatory processes. *Trends in Ecology & Evolution*, **30**, 513–515.

Côté, I.M., **Darling, E.S.** & **Brown, C.J.** (2016) Interactions among ecosystem stressors and their importance in conservation. *Proceedings of the Royal Society B: Biological Sciences*, **283**, 20152592.

de Souza Machado, A.A., **Lau, C.W.**, **Kloas, W.**, **Bergmann, J.**, **Bachelier, J.B.**, **Faltin, E.** ***et al.*** (2019) Microplastics can change soil properties and affect plant performance. *Environmental Science & Technology*, **53**, 6044–6052.

de Souza Machado, A.A., **Wood, C.M.** & **Kloas, W.** (2019) Novel concepts for novel entities: updating ecotoxicology for a sustainable anthropocene. *Environmental Science & Technology*, **53**, 4680–4682.

Eisenhauer, N., **Hines, J.**, **Maestre, F.T.** & **Rillig, M.C.** (2023) Reconsidering functional redundancy in biodiversity research. *npj Biodiversity*, **2**, 1–4.

Felton, A.J. & **Smith, M.D.** (2017) Integrating plant ecological responses to climate extremes from individual to ecosystem levels. *Philosophical Transactions of the Royal Society B: Biological Sciences*, **372**, 20160142.

Gamelon, M., **Jenouvrier, S.**, **Lindner, M.**, **Sæther, B.-E.** & **Visser, M.E.** (2023) Detecting climate signals cascading through levels of biological organization. *Nature Climate Change*, **13**, 985–989.

Gunderson, A.R., **Armstrong, E.J.** & **Stillman, J.H.** (2016) Multiple stressors in a changing world: the need for an improved perspective on physiological responses to the dynamic marine environment. *Annual Review of Marine Science*, **8**, 357–378.

Jackson, M.C., **Pawar, S.** & **Woodward, G.** (2021) The temporal dynamics of multiple stressor effects: from individuals to ecosystems. *Trends in Ecology & Evolution*, **36**, 402–410.

Legrand, D., **Guillaume, O.**, **Baguette, M.**, **Cote, J.**, **Trochet, A.**, **Calvez, O.** ***et al.*** (2012) The Metatron: an experimental system to study dispersal and metaecosystems for terrestrial organisms. *Nature Methods*, **9**, 828–833.

Orr, J.A., **Rillig, M.C.** & **Jackson, M.C.** (2022) Similarity of anthropogenic stressors is multifaceted and scale dependent. *Natural Sciences*, **2**, e20210076.

Orr, J.A., **Vinebrooke, R.D.**, **Jackson, M.C.**, **Kroeker, K.J.**, **Kordas, R.L.**, **Mantyka-Pringle, C.** ***et al.*** (2020) Towards a unified study of multiple stressors: divisions and common goals across research disciplines. *Proceedings of the Royal Society B: Biological Sciences*, **287**, 20200421.

Paine, R.T., **Tegner, M.J.** & **Johnson, E.A.** (1998) Compounded perturbations yield ecological surprises. *Ecosystems*, **1**, 535–545.

Pascual, L.S., **Mittler, R.**, **Sinha, R.**, **Peláez-Vico, M.Á.**, **López-Climent, M.F.**, **Vives-Peris, V.** ***et al.*** (2023) Jasmonic acid is required for tomato acclimation to multifactorial stress combination. *Environmental and Experimental Botany*, **213**, 105425.

Peláez-Vico, M.Á., **Sinha, R.**, **Induri, S.P.**, **Lyu, Z.**, **Venigalla, S.D.**, **Vasireddy, D.** ***et al.*** (2023) Integrative phenotypic-transcriptomic analysis of soybean plants subjected to multifactorial stress combination, 2023.08.15.553447. Available from: https://www.biorxiv.org/content/10.1101/2023.08.15.553447v1 [Accessed 5th October 2023].

Rillig, M.C., **Lehmann, A.**, **Orr, J.A.** & **Waldman, W.R.** (2021) Mechanisms underpinning nonadditivity of global change factor effects in the plant–soil system. *New Phytologist*, **232**, 1535–1539.

Rillig, M.C., **Ryo, M.** & **Lehmann, A.** (2021) Classifying human influences on terrestrial ecosystems. *Global Change Biology*, **27**, 2273–2278.

Rillig, M.C., **Ryo, M.**, **Lehmann, A.**, **Aguilar-Trigueros, C.A.**, **Buchert, S.**, **Wulf, A.** ***et al.*** (2019) The role of multiple global change factors in driving soil functions and microbial biodiversity. *Science*, **366**, 886–890.

Rillig, M.C., **van der Heijden, M.G.A.**, **Berdugo, M.**, **Liu, Y.R.**, **Riedo, J.**, **Sanz-Lazaro, C.** ***et al.*** (2023) Increasing the number of stressors reduces soil ecosystem services worldwide. *Nature Climate Change*, **13**, 478–483.

Sage, R.F. (2020) Global change biology: a primer. *Global Change Biology*, **26**, 3–30.

Simmons, B.I., **Blyth, P.S.A.**, **Blanchard, J.L.**, **Clegg, T.**, **Delmas, E.**, **Garnier, A.** ***et al.*** (2021) Refocusing multiple stressor research around the targets and scales of ecological impacts. *Nature Ecology & Evolution*, **5**, 1478–1489.

Sinha, R., **Peláez-Vico, M.Á.**, **Shostak, B.**, **Nguyen, T.T.**, **Pascual, L.S.**, **Zandalinas, S.I.** ***et al.*** (2022) The effects of multifactorial stress combination on rice and maize, 2022.12.28.522112. Available from: https://www.biorxiv.org/content/10.1101/2022.12.28.522112v1 [Accessed 5th October 2023].

Speißer, B., **Wilschut, R.A.** & **van Kleunen, M.** (2022) Number of simultaneously acting global change factors affects composition, diversity and productivity of grassland plant communities. *Nature Communications*, **13**, 7811.

Thorogood, R., **Mustonen, V.**, **Aleixo, A.**, **Aphalo, P.J.**, **Asiegbu, F.O.**, **Cabeza, M.** ***et al.*** (2023) Understanding and applying biological resilience, from genes to ecosystems. *npj Biodiversity*, **2**, 1–13.

Vitousek, P.M. (1994) Beyond global warming: ecology and global change. *Ecology*, **75**, 1861–1876.

Zandalinas, S.I., **Fritschi, F.B.** & **Mittler, R.** (2021) Global warming, climate change, and environmental pollution: recipe for a multifactorial stress combination disaster. *Trends in Plant Science*, **26**, 588–599.

Zandalinas, S.I., **Sengupta, S.**, **Fritschi, F.B.**, **Azad, R.K.**, **Nechushtai, R.** & **Mittler, R.** (2021) The impact of multifactorial stress combination on plant growth and survival. *New Phytologist*, **230**, 1034–1048.