Forest Ecology and Management xxx (xxxx) xxx–xxx

Contents lists available at ScienceDirect

Forest Ecology and Management

journal homepage: www.elsevier.com/locate/foreco

Community-based biotic effects as determinants of tree resistance to pests and pathogens

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ARTICLE INFO

Keywords:
Associational resistance
Induced resistance
Hybridisation
Endophytes
Mycorrhiza
Host genotype

ABSTRACT

In the light of the global increase in forest pests and diseases, accompanied by withdrawal of chemical pesticides and fungicides, we review recent advances in how forest tree resistance to pests and diseases might be influenced by manipulation of characteristics of the trees' community of associated plants and other organisms. These include associational resistance (AR), effected by manipulation of tree species composition or richness, genotypic diversity, or by tree density/frequency of resistant species or genotypes, use of hybrids, and strategic use of bacterial and fungal symbionts to engender systemic induced resistance, or defense priming. Due to the rotation times in forest production systems, none of the community-based actions that attempt to disrupt a tree-pest or tree-pathogen interaction, can be used in a rapidly mobilised targeted response to currently known pests or pathogens or to unknown ones that are yet to emerge. The only exception is the possible use of non-pathogenic or mutualistic organisms to induce systemic resistance or prime tree defence systems against attack. Due to the range of permutations of participating species and assemblages and the idiosyncratic nature of their ecological interactions and processes, it is not currently possible to formulate predictive rules to protect forests using only these community-based methods. It is however possible to use them as part of a long-term prophylactic strategy by structuring future forests to increase their general resistance, and reduce the probability of impacts of pests and diseases, e.g. via diversification of tree species and genotypes.

1. Introduction

In recent years there has been a rapidly increasing number of pests and pathogens of plants in agriculture and forestry, due to colonisation or translocation of either the pest or its host into new global regions (e.g. UK, DEFRA, 2013), facilitated by globalization and climate change. This exceptional situation and the increasing awareness of the threat these and other spreading organisms pose to many native and exotic tree species globally, has coincided with reductions in the use of pesticides, fungicides and herbicides, increasingly via bans supported by legislation (Bellinder et al., 1994; Neumeister, 2007). The development of environmentally sustainable novel approaches to protect trees, woodlands and forests is therefore a high priority. In this review we assess recent advances in how tree resistance to pests and diseases might be influenced by manipulation of characteristics of the forest plant community, and by possible interactions among pests and/or pathogens and with other organisms. Such approaches are complementary to and likely to be implemented in conjunction with biotechnological solutions and other silvicultural approaches as part of integrated pest management strategies (Waring and O'Hara, 2005). The focus here is on how the community of organisms associated with a tree might influence its resistance to pests or pathogens. In particular we consider how the tree's community of other higher plants and associated assemblages might determine its propensity to avoid attack by or survive in the presence of the pest or pathogen, rather than on other components of resistance, namely the plants' ability to either tolerate or recover from the pathogen attack. Examples are used from temperate and boreal forest systems where possible, but we draw on experience from other environments and non-tree species, which illustrate particular principles involved in how interactions with other organisms can affect the resistance of a particular tree species to pests and pathogens.

We ask, what is the role of host plant ecological interactions with other organisms as determinants of forest resistance to tree pathogens and pests? We consider likelihood of herbivore attack, or transmission of disease, or other modifications of susceptibility or resistance. We review recent developments in these broad subject areas, and identify which community-ecology based processes have the potential to ultimately result in the application of novel long-term community-based

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https://doi.org/10.1016/j.foreco.2018.01.037
Received 4 October 2017; Received in revised form 18 January 2018; Accepted 20 January 2018
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solutions to increase forest resistance to pests and pathogens. Resistance, along with resilience, which is an individual's or system's propensity to recover following disturbance, are the two components of the stability, and therefore the sustainability of an ecosystem (Grimm and Wissel, 1997; Nunez-Farfan et al., 2007). Our focus is primarily on ecological and epidemiological processes which underpin recommendations for forest management in response to existing pests or pathogens, or as a prophylactic against newly emerging or imminent threats. These processes also form the basis of evolutionary adaptation and co-evolution of the tree hosts with their pests and pathogens which ultimately determines the longer-term adaptation and resistance of the forest and its constituent trees (Day and Gandon, 2007).

2. The effects of plant diversity on resistance

In general, species-rich plant communities are likely to be more resistant to invasive herbivores because of their increased diversity and abundance of natural enemies of invertebrate pests (Hooper et al., 2005). Overall maintenance of insect and bird diversity in planted forests, including agroforestry systems, is likely to contribute to stability and limit outbreaks of pests and pathogens; increasing diversity of tree species is a means to achieve this (Stamps and Linit, 1997; Vehvilainen et al., 2007). As well as indirectly influencing these 'top-down' regulatory mechanisms emanating from higher trophic levels, mixtures of tree species can exert 'bottom-up' disruptive influences on accessibility to, and perception and host-finding by herbivores (Moreira et al., 2016). We consider these processes in more detail below.

2.1. Tree species diversity and associational resistance to herbivores

The well documented phenomenon of associational resistance (AR) refers to decreased herbivory experienced by a plant growing with heterospecific neighbours. This is otherwise known as 'associational defence' (Atsatt and O'Dowd, 1976), 'neighbour contrast defence' (Alm Bergvall et al., 2006) or 'associational refuge' (Wahl and Hay, 1995). The converse is referred to as 'associational susceptibility' (AS) or 'shared doom' (Wahl and Hay, 1995) in which susceptibility of the focal plant species increases as a result of association with a more susceptible species. Associational resistance can be intentionally achieved by creating a specific mixture of tree species to counter pests. The basic processes underlying associational resistance probably also occur when general species richness is increased without specification or planning of which herbivore's effects might be disrupted. In these circumstances, other factors such as species richness and abundance of predators and parasitoids are also likely to change.

Several studies attribute the bottom-up effects of AR to the inhibition of host-finding by the herbivore in tree mixtures due to some kind of physical impediment or olfactory confounding of detection, location or stimulation of feeding or egg-laying on the preferred tree species. These can occur even in specialist insects (Jactel et al., 2011; Castagneyrol et al., 2013; Castagneyrol et al., 2014b; Guyot et al., 2015) which are especially closely adapted to cues provided by their hosts. Additionally, the detoxification limitation hypothesis predicts that generalist herbivores are limited in their intake of a particular species by their rates of detoxification of specific plant secondary metabolites. This means that they should diversify their diet, where possible, to avoid overloading a particular detoxification pathway. This means that they concomitantly inflict less damage to a single plant species within the mixture, and is applicable to both mammalian and insect herbivores (Singer et al., 2002; Marsh et al., 2006). Other mechanisms facilitating AR in tree species mixtures include the disruption of specific host-finding and olfactory mechanisms of pests, and promotion of top-down interactions from predators or parasitoids (Hambäck et al., 2000).

Whether the outcome of mixing tree species is in favour of AR or AS with respect to a particular focal tree species, is determined by the relative preference of the herbivore for the focal versus the alternative species, and their colonisation and foraging processes (White and Whitham, 2000; Bergman et al., 2005; Milligan and Koricheva, 2013; Hambäck et al., 2014; Stutz et al., 2015). So, the response varies among combinations of tree species, and among feeding-guilds (Vehvilainen et al., 2007), the response of which gives a pointer to the likely response of its trophically similar member species. The AR/AS responses of pine sawflies (*Neodiprion sertifer*) and pine crown aphid (*Cinara pinea*) populations in Scots pine (*Pinus sylvestris*)/silver birch (*Betula pendula*) mixtures, were both strongly affected by ant predation. It was consequently suggested that AR should be considered as a system trait, arising from a combination of ecological participants and circumstances that determines the system's overall general resistance to herbivore damage (Kaitaniemi et al., 2007).

The herbivores considered in most studies of AR or AS are mainly mammals and insects. Initial studies, including comparative studies found no clear consensus, but considered AR to be the most likely outcome for mammalian herbivores and AS for insect herbivores (Barbosa et al., 2009; Axelsson and Stenberg, 2012; Milligan and Koricheva, 2013; Cook-Patton et al., 2014; Herfindal et al., 2015). These studies focused in particular, on host-finding by herbivores and host plant vulnerability and apparency to the herbivores. Contrary to this general finding of AS in insect herbivores, overall levels of insect damage are lower in mixed forests (Castagneyrol et al., 2014a; Castagneyrol et al., 2014b; Conner et al., 2014; Guyot et al., 2015; Guyot et al., 2016). This suggests that factors other than simply AR/AS relationships of hosts and insects are contributing to the overall outcome or that insects cannot be considered as a single group in this regard. Closer inspection of the herbivores' feeding strategy has shed further light on this. Associational susceptibility or no effect of tree species mixture has been the usual result when considering generalist insect herbivores (White and Whitham, 2000; Jactel and Brockerhoff, 2007; Plath et al., 2012). However, for specialist insects, inconsistency and unpredictability of the AS versus AR outcomes have been attributed to differential insect species-responses to host dilution by associated, less-preferred forest tree species (Plath et al., 2012). A recent meta-analysis has clarified that for specialist insects, where AR occurred it was influenced strongly by the relative abundance of their preferred species, independent of the phylogenetic difference between available tree species, whereas generalist herbivores experienced AR only when the contrasting species were phylogenetically distant (Castagneyrol et al., 2014a).

It seems to be a general rule that any beneficial effects of tree species diversity for forest resistance against pests can be over-ridden when generalist pest populations reach high abundance (White and Whitham, 2000). In a study of tree species richness on vole (*Microtus* spp. and *Clethrionomys* spp.) and moose (*Alces alces*) damage, moose browsing increased with tree species diversity. In contrast, and again associated with their different foraging strategy, damage due to voles decreased with increasing tree species diversity, but the effect of tree-species diversity on vole damage was stronger in years of high vole abundance (Vehvilainen and Koricheva, 2006). Over-riding of defences when herbivores are abundant also applies when considering genotypes within a species that have contrasting resistance traits, e.g. quaking aspen *Populus tremuloides*, which can be swamped by abundant defoliating caterpillars (Donaldson and Lindroth, 2008). This reveals limitations to the applicability of diversification as part of a strategy to manage resistance to pests for which outbreaks in numbers might occur, particularly during the years of establishment of a mixed species forest. This review highlights the level of detailed knowledge required, on feeding-guilds, species-specific population dynamics and ecological processes, to predict the outcome and effectiveness of increasing tree diversity to promote forest resistance.

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