Light Spectral Quality, Phytochrome and Plant Competition

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The light environment experienced by plants in natural vegetation is strongly dependent upon interactions with neighbors. For plants in dense stands, reduced irradiance can lead to reductions in growth and fitness. Spectral light quality is also altered beneath a leaf canopy, and can serve as an important signal of competition for light. Recent physiological studies indicate that plants can perceive the quality of light reflected from neighbors as an accurate predictor of future competition, and respond morphologically even before they are directly shaded. These findings have important implications for plant population biology, and provide a valuable opportunity for the study of adaptive plasticity.

Light is a critical resource for plants, and competition for light can result in reduced growth and reproduction. Morphological and physiological responses of plants to high and low irradiance have been extensively investigated, constituting one of the classic examples of plasticity in the physiological literature[1]. In most of these studies, irradiance has been reduced experimentally with neutral shade, contrasting plants from open habitats with those from forest understories. Under natural conditions, however, plants beneath a leaf canopy experience not only a reduction in irradiance but also altered spectral light quality due to the selective filtering of blue and red wavelengths by chlorophyll. In particular, the red to far-red ratio (R:FR) of incident light may be dramatically reduced under a closed leaf canopy compared with values in full sunlight, and may also vary widely as a function of canopy density, depth and age[2]. Thus, R:FR is an important cue by which plants may detect microenvironmental variation in vegetation shade, both from overstory foliage and from neighbors[2]. This cue may be particularly important for plants that grow in dense stands in non-forested habitats, since in the absence of overstory shade, light quality will be an indicator of competition with neighbors for light.

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Phytochrome as a detector of vegetation shade

Plant perception of R:FR is mediated by phytochrome, a family of photoreceptors that convert reversibly between two forms when exposed to red or far-red light (see Box 1). It has been proposed that the primary ecological function of phytochrome in green plants is to act as a sensitive sensor of vegetation shade[2]. Phytochrome-mediated morphogenesis in light-grown plants is a function of the photoequilibrium between the two forms, resulting in a sensitive, graded morphological response to light spectral quality over the range of R:FR values typical of vegetation shade[2]. Recently the role of different phytochrome species in this response has been directly investigated using phytochrome mutants[7,8]. Many plant species typically respond to reduction in the R:FR of incident light with increased apical dominance, manifested in decreased branching, stem extension and internode elongation[2,9] (Fig. 1). In grasses, low R:FR suppresses tillering[10,11]. Light quality can also cause changes in traits such as petiole length, leaf area or specific leaf weight[12,13]. Shade-tolerant species, such as forest understory herbs, are thought to be less responsive to R:FR than species from open habitats[9], although surprisingly few studies have been conducted to test this hypothesis. In many plant species, phytochrome also regulates seed responses to light[2]. Germination is often suppressed by foliage shade[14], and lower R:FR during seed maturation may induce a light requirement for germination[15].

Plastic response of plants to density

At the same time that direct evidence has mounted for phytochrome-mediated morphological response to light quality, plant population biologists and foresters have observed similar plastic

response of plant architecture to increasing density. In crowded plants, branching is reduced, height is increased (relative to biomass, stem diameter and leaf area), and the distribution of leaves is shifted to the top of the canopy[16–20]. In several species, the allometric increase in height with biomass, stem diameter, and/or leaf area is steeper, and branching is more suppressed, for smaller plants within dense stands[17–19] (Fig. 2). This suggests that the magnitude of these effects may be greater for plants shaded beneath the canopy. Although these studies did not directly investigate the relationship between competition and light quality, the morphological responses observed are consistent with the results of experiments manipulating R:FR, and suggest that many plant responses to density in natural populations may often be phytochrome mediated.

Light quality as a predictor of competition

An interesting and important result from recent physiological studies is that typical morphological responses to crowding can be induced by changes in the R:FR, not only of direct incident light but also of light reflected by neighbors, even before direct shading occurs[21–24]. There is strong evidence that these responses are phytochrome mediated, and are largely due to R:FR perceived locally in the stem, although it has recently been suggested that reduced irradiance at the level of the internodes may also play a role[25]. Reflected light quality appears to be a reliable signal of the presence and proximity of neighbors[21–26]. Even before there is a measurable reduction in photosynthetically active radiation within a growing stand, the R:FR of light reflected onto stems decreases with neighbor proximity[21–26]. This has been explicitly demonstrated using

Box 1. Phytochrome

The term phytochrome refers to a family of photoreceptors, each consisting of a low molecular weight protein covalently attached to a photoreversible pigment. These photoreceptor molecules can be induced to shift between P_r (red absorbing form) and P_{fr} (far-red absorbing form) when exposed to red (660 nm) or far-red light (730 nm), respectively.

Red Light

$$P_r \rightleftarrows P_{fr} \longrightarrow Response$$

Far Red Light
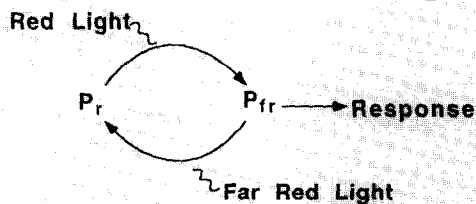
Increases in the red to far-red ratio (R:FR) experienced by plants produce a continuum of proportional increases in the relative concentration of P_{fr}, and thus in the phytochrome photoequilibrium, P_{fr}:P (the ratio of P_{fr} to total phytochrome). The sensitivity of phytochrome photoequilibrium to R:FR is greatest over the range of R:FR values typical of canopy shade[2]. The magnitude of phytochrome-mediated morphological response in light-grown plants is often a linear function of P_{fr}:P; thus, the sensitivity of phytochrome photoequilibrium to R:FR can produce graded morphogenetic responses to the range of variation in light quality found in natural vegetation[2]. The involvement of phytochrome in developmental morphogenesis is easily demonstrated, simply by studying R:FR responses of a given function.

Phytochromes are found throughout the plant kingdom. They play an important role in gene regulation[3–5], and control a wide variety of developmental processes, including seed germination, photoperiodic flowering responses, seedling de-etiolation, biosynthesis of chlorophyll and other pigments, and morphogenetic responses to light[6]. Different functions are regulated by different molecular species of phytochrome, which are encoded by different genes[4,5]. Phytochrome can be isolated, purified and assayed, both spectrophotometrically *in vivo* and *in vitro* and by immunological techniques. Photomorphogenetic mutants and transgenic plants are now being used to elucidate mechanisms of gene action[3–5]. Until recently, most studies were done in etiolated plants; however, it is now known that there are two species of phytochrome. Type I, which predominates in etiolated tissues and degrades rapidly in the P_{fr} form, has been extensively studied. Type II, which exists in low abundance in etiolated tissues and is more stable in the P_{fr} form, predominates in green tissues, and appears to be more important for morphogenesis in green plants[4,5].

fiberoptic probes inserted directly into plant stems[26]. Moreover, stem elongation is induced by neighbors even at high irradiance[24]. Elongation is stimulated when the R:FR reaching the stem is reduced by selective mirrors with high FR reflectance[21] or annular filters that absorb R wavelengths[25,27]. The elongation response does not occur if neighboring plants are bleached[21], and is suppressed in dense stands if the R:FR of reflected light is reduced with cuvettes containing $CuSO_4$ solutions (which specifically absorb FR light)[22,27]. Similarly, reduced R:FR reflected by neighbors reduces tillering in grasses[10], and this response is reversed in dense canopies by supplementary red light at the base of the culm[28]. Manipulation of reflected light quality has also been used to demonstrate that seedlings of *Portulaca oleracea*, a recumbent weed, employ R:FR as a cue to avoid growing in the direction of neighbors[29]. This mounting experimental evidence is consistent with the suggestion that a critical function of phytochrome in green plants may be predicting light competition and triggering morphological responses to avoid future shading[21,30].

Implications of plastic response to light quality for plant competitive interactions

If phytochrome-mediated perception of light quality plays an important role in the plastic response of wild plants to crowding, it has significant implications for competitive dynamics of natural plant populations. It has been suggested that, under competition for light, plant architecture may have an important impact on size hierarchy development and self-thinning dynamics[17,31]. If so, species differences in the capacity to sense and respond morphologically to neighbors could have a critical impact on plant population dynamics. Species that respond with stem elongation and decreased branching to low R:FR should have less hierarchical size distributions and less self-thinning in dense stands than species in which allometry is unresponsive to light quality. The experimental techniques used by plant physiologists to manipulate morphology in dense stands by altering spectral light quality may prove extremely useful in elucidating the mechanisms of plastic response to density in natural plant populations.

Response to light spectral quality may also influence interspecific interactions. For example, it has been suggested that light quality may play a role in the suppression of summer annuals in successional old fields[32]. Moreover, R:FR may actually provide information about the identity of competing species[12]. When *Trifolium repens* was grown under canopies of three grass species at similar levels of irradiance, plastic responses such as suppression of growth and branching and elongation of leaf petioles were strongest under *Holcus lanatus*, the species producing the largest reduction in R:FR[12]. Thus, light quality may be an important determinant of morphological responses to interspecific competition. Phytochrome-mediated species differences in germination response to microenvironmental heterogeneity in R:FR may also play an important role in community dynamics[14]. The ability of dormant seeds to detect gaps in established vegetation may be important for the persistence of annual species in perennial communities[33].

Is plastic response to light quality adaptive?

It has been suggested that sensitivity to reflected R:FR light, before actual shading, is adaptive because it enables plants to anticipate and avoid competition for light[21–24,30]. This is an ecologically important, testable hypothesis that deserves particular attention in light of current theoretical and empirical interest in the evolution of phenotypic plasticity[34]. Plasticity of a given trait can only be considered adaptive if it results in high relative fitness in all environments[34]. To support the hypothesis that plastic response to reflected light quality is adaptive in a given species it is necessary to demonstrate that: (1) the morphology induced by low R:FR reflected from neighbors increases relative fitness at high density; and (2) the same morphology is selected against in uncrowded plants[30].

Both predictions are plausible. Recently, strong evidence has mounted that asymmetric competition, in which large individuals are disproportionately successful in capturing resources and thus,

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suppress the growth of smaller individuals, may be an important mechanism generating hierarchical size distributions in plant populations[16,17,35–37]. In particular, it has been suggested that competition for light will be asymmetric, since taller plants can shade smaller individuals[17,35,36]; light availability to leaves declines and becomes more variable with crowding[20]. Since plant size is strongly related to fitness, any trait conferring an early competitive advantage should be strongly selected for by asymmetric competition[37,38]. Thus early shoot elongation and high apical dominance triggered by phytochrome perception of neighbors might provide an important fitness advantage in crowded conditions, by increasing the chance that a plant will reach the top of the canopy and escape suppression by taller plants.

It is also reasonable to predict that stem elongation and suppressed branching may be disadvantageous when plants are not crowded. Resource allocation to height at the expense of photosynthetic leaf biomass might reduce growth rate in the absence of competition[39], and tall, slender stems will be at greater risk for breakage or falling over. Moreover, if growth and reproduction are limited by meristem production, rather than by resource availability, suppression of branching could reduce growth[17] and the capacity for later reproduction[40].

If the adaptive plasticity hypothesis is correct, variation in the intensity of light competition should result in disruptive phenotypic selection on plant morphology at different densities or for plants in the leaf canopy and individuals suppressed beneath it. Early detection of neighbors followed by plastic morphological response therefore should be highly advantageous when competition intensity is unpredictable and light quality is a reliable cue of future shade. However, it has been suggested that stem elongation in response to reduced R : FR may be less advantageous for shade-tolerant woodland plants, which cannot overtop the overstory canopy, than for plants of open habitats[9].

Experimental manipulations of plant phenotype

To our knowledge, no experiments have explicitly tested these predictions in an evolutionary context by examining the impact of phytochrome responses on fitness in natural populations. However, several studies have examined functional aspects of the elongation response to neighbors. In *Datura ferox*, seedlings previously grown at low density and transferred to high-density stands intercepted lower levels of photosynthetically active radiation than their elongated neighbors, but the reverse transfer was not performed and fitness consequences were not examined[24]. Ballaré *et al.*[27] performed a series of experiments to examine the cost to leaf and root growth of biomass allocation to stem elongation in dense stands of *Amaranthus quitensis*. To suppress the elongation response in dense stands, they grew whole canopies of plants under cuvettes of $CuSO_4$ solution which selectivelyabsorbed far-red radiation, raising the R : FR of light reaching the plants; these plants were compared with control plants grown under neutral filters. In addition, isolated plants were grown with internodes covered by annular filters that reduced the R : FR of light reaching the stem, promoting elongation. In both experiments, elongated plants had greater stem biomass and consequently greater total biomass than non-elongated plants, and there

Fig. 1. Morphological response of *Impatiens capensis* seedlings to reductions in irradiance and R : FR. Seedlings were exposed to three light treatments: open (covered with transparent plastic sheets, which transmitted full sunlight and a R : FR of 1.1); neutral shade (covered with neutral shade cloth, which reduced irradiance to 6% of incident light without altering R : FR); and leaf shade (covered with a layer of living banana leaves, which reduced irradiance to 6% and R : FR to 0.2). Comparison of the two shade treatments provides a test for the effect of light quality, controlling for irradiance; comparison of the high irradiance and neutral shade treatments provides a test for the effect of irradiance, independent of light quality. Note that dry biomass accumulation did not differ between the two shade treatments, but that stem and internode elongation was increased, and the ratio of leaf area to stem height was decreased, by reduced R : FR. Different letters indicate significant treatment differences (P < 0.05). From data in Ref. 49.
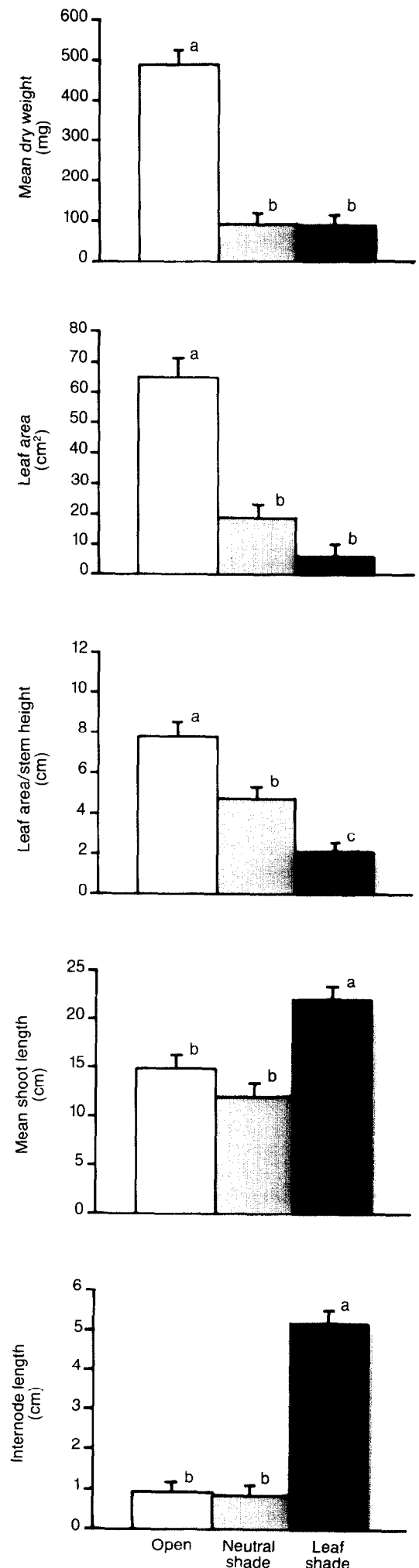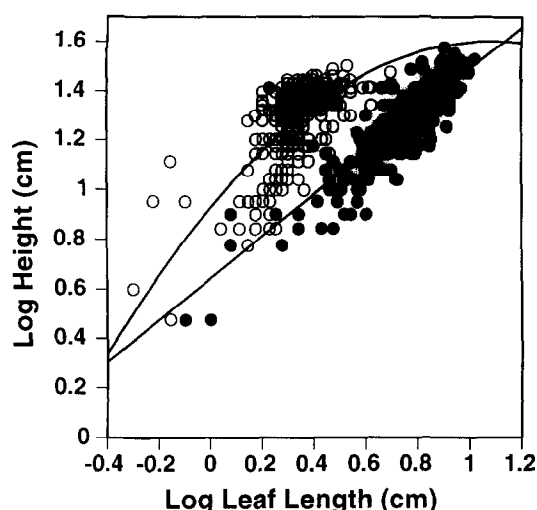
Fig. 2. Effect of density on the allometric relationship of plant height and length of the longest leaf in a natural stand of *Impatiens capensis* seedlings. Plots were thinned to 100 seedlings m^{-2} (open circles) or left at natural density of 2563 m^{-2} (filled circles). High density induced greater stem elongation relative to maximum leaf size, similar to that induced in the same species by decreased R : FR in Fig. 1. The allometric relationship was linear for plants in the thinned treatment. However, at high natural density, the relationship was significantly curvilinear, with a steeper slope for smaller plants, suggesting that position within the canopy has a qualitative effect on plant shape. Weiner et al.[18] and Weiner and Thomas[19] obtained strikingly similar results for the relationships between height and total leaf area, biomass and stem diameter in the closely related species, *I. pallida. Redrawn from Ref. 16, after Ref. 19.*

was no evidence that allocation to stem tissue resulted in decreased allocation to leaves or roots.

This study did not examine the long-term fitness consequences of elongation. If early stem growth rate is strongly related to fitness in natural populations, the observation that elongation provided a growth advantage in dense stands would support the first prediction of the adaptive plasticity hypothesis, but the fact that elongation also increased growth in isolated plants would falsify the second prediction. However, it seems likely that in natural populations elongated plants might have reduced fitness at low density due to opportunity costs of suppressed branch[40] or increased risk of stem structural failure.

Experimental tests of the hypothesis that plastic response to light quality is adaptive in natural populations are clearly needed. The ability to manipulate plant phenotype by altering light quality provides a potentially powerful tool for addressing this issue. For example, the relative fitness of experimental plants with 'appropriate' and 'inappropriate' phenotypes could be compared both at low density and in dense canopies. It is also important to determine

whether the strength and direction of natural selection on traits that respond plastically to light quality differs among light environments in the predicted direction in natural populations. This question can be addressed using demographic techniques for phenotypic selection analysis[41-43].

Is there genetic variation for plastic response to light quality?

For adaptive plasticity to evolve in response to selection in heterogeneous environments, genotypes within populations must vary in reaction norms, that is, in phenotypic response to a given range of environments[34,44]. Virtually nothing is known about the nature of genetic variation for plastic response to light quality within natural plant populations. Recent studies of mutants aberrant in developmental response to light[4,5,45] suggest that variation at phytochrome loci or the genes they regulate could potentially produce genetic variation in reaction norms of plants to light quality. There is evidence that wheat cultivars differ in responses to end-of-day irradiation with red or far-red light[46]. The single study to investigate genetic variation in response to leaf shade in wild plants detected significant differences between two *Trifolium repens* clones in morphological response to foliage versus neutral shade, suggesting that such variation is indeed possible[47]. If such genetic variation exists within plant populations, it could potentially provide a critical substrate for heterogeneous density-dependent selection. There is also very little information available about population differences in sensitivity to light quality. If selection for sensitivity to R : FR is stronger in open habitats than beneath forest canopies, the possibility exists for ecotypic differentiation in plastic response to light quality. Few data exist to test this prediction (but see Ref. 9).

Response to light quality as a system for studying adaptive plasticity

Recently there has been a surge of theoretical and empirical interest in the evolutionary implications of phenotypic plasticity. However, despite this interest relatively little

is known about the genetic basis of plasticity or its fitness consequences in natural plant populations. Plastic response to light quality is particularly interesting in this context because mechanisms of gene action and regulation are being intensely studied at the molecular level[3-5], and the physiological responses are well characterized. In addition, the ecological context is well defined, and manipulative experiments can be performed to examine directly the fitness consequences of the plastic response. Research at the interface between plant physiological ecology and population biology can provide important insights into the evolution of plant function[48]. Phytochrome-mediated responses to light quality provide an excellent opportunity for integrating genetic, physiological and population biology perspectives to the study of adaptive plasticity.

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Disturbance of the Phosphorus Cycle: A Case of Indirect Effects of Human Activity

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Phosphorus (P) often limits primary productivity of aquatic systems. Humans have altered the P cycle in aquatic systems, directly, by mining P-rich rock, and indirectly, through the manipulation of other element cycles and the alteration of aquatic food webs. Aquatic ecologists are becoming increasingly aware of the importance of these indirect alterations to biogeochemical cycles. Quantitative predictions of these indirect effects will be an important focus of future studies.

Humans have caused severe alterations to biogeochemical cycles[1,2]. While some of these alterations are relatively direct, others are very indirect, being mediated through several interacting biological or chemical changes. However, the indirect effects of humans on biogeochemical cycles can be as severe as the direct effects and owing to the complex interactions involved, they are often overlooked. The phosphorus cycle exemplifies a biogeochemical cycle that has been severely altered by human activity.

Phosphorus cycling and direct human impact

Phosphorus is a critical part of living matter. It is contained in phospholipids of cell membranes, in ATP and in DNA. The high energy bond in PO_4 is crucial to the maintenance of the animated world[3]. Whether P

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defines life itself or not, all organisms require P and autotrophic organisms must obtain this P from the environment. Acquisition of P can be energetically expensive because of the extremely low concentration of available P found in many environments. For example, in a typical freshwater lake the available P concentrations in the surrounding water is 0.0001 times that in the typical cell. For comparison, carbon, sulfur and nitrogen are on average 2.5 to 100 times more concentrated in these same freshwater environments with respect to cell requirements[4].

The importance of P to cell functions, coupled with its relatively low availability, is the reason why P fertilization can enhance autotrophic production. Thus, P is a critical component of plant fertilizers. The mining of P-rich rock to produce these fertilizers has provided a large quantity of available P for agricultural land. Much of this P eventually reaches lakes, streams and ultimately the sea via rivers (Fig. 1). It has been estimated that on a global scale the mining of P-rich rock has more than doubled the supply of P to coastal seas, as

compared to preindustrial levels[5]. In heavily populated and agricultural areas this effect is greater and many lakes have P-loading 10–100 times greater than preindustrial levels. This enhanced P-loading has led to increased productivity in many aquatic systems, resulting in some becoming eutrophic or hypereutrophic. Hypereutrophic waters are often characterized by foul smelling algal scums, hypoxic conditions (which lead to fish death) and blooms of poisonous algae. Thus, the direct effect of human activity on the P cycle is severe, and in many cases obvious and unappealing. Therefore, these direct effects have been the subject of much research and policy attention[6].

Indirect human impact

Phosphorus is an extremely active element biologically and chemically. Chemically it interacts strongly with the iron, aluminium and calcium cycles. Biologically it is taken up directly from the environment by not only photoautotrophs but also by chemotrophs and heterotrophic bacteria and fungi. Given these multiple interactions it is not surprising that human activity