

Grass endophytes as a model*

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The importance of the role of grass endophytes in assisting the growth and persistence of temperate grasses present in pastoral agriculture, native grasslands and turf is becoming recognised. This paper reviews the salient facts known about grass endophytes and their relationships with their hosts. The compounds that endophytes synthesise in their host affect not only the biology of the grass but also influence the pests, diseases and the animal herbivores which feed on it. The selection of special strains of endophytes which overcome some of the aspects of endophytes which are not welcomed by farmers will be discussed. Many grass endophytes can only be transmitted as mycelium in seed and this is in contrast to fungal endophytes of most other plants. In spite of the differences in life cycles of endophytes in grasses and those in other species of plants the knowledge gained from grass endophyte research should be of assistance to researchers of endophytes in other plants.

Key words: Clavicipitaceae, ecology, *Acremonium*, *Epichloe*, *Neotyphodium*

Endophytic fungi are, as the name suggests, fungi which live for some or all of their life cycle within plants. Thus they may be parasitic such as the smut fungi, or non-aggressive while the plant is growing well, or mutualistic as is the case with many grass endophytes. Some endophytes of grasses such as *Epichloe* species may even have both parasitic and mutualistic phases in their life cycle. In recent years the term endophyte has been narrowed somewhat in its usage and Wilson (1995) proposes that endophyte now describes not only the location but also the type of infection strategy of the fungus or bacterium. He suggests that endophytes may be fungi or bacteria which have dormant or latent stages within plant tissues prior to causing disease symptoms. Endophytes of grasses which have no perfect stage lie slightly outside this definition because they are not known to cause plant diseases but are in a mutualistic relationship with their host.

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Classification and life cycle

Endophytic fungi of grasses are classified in the family Clavicipitaceae and include the genera *Epichloe*, *Balansia*, *Atkinsonella*, *Myriogenospora* and *Echinodithis* (White, 1997). Most research into grass/endophyte relationships has been with members of the genus *Epichloe* and with fungi thought to be related to *Epichloe* but which do not have a sexual stage in their life cycle. These asexual endophytes were originally classified as *Acremonium* species (Morgan-Jones & Gams, 1982) but are now reclassified as *Neotyphodium* (Glenn & al., 1996). Results from studies by An & al. (1992) and Schardl & al. (1991) who compared sequences of the internal transcribed spacers of nuclear rRNA genes suggest that *Neotyphodium* species originated from *Epichloe* species but they have lost their sexual stage. It is on these *Neotyphodium* endophytes that most of the grass/endophyte research has concentrated.

Grasses infected with *Neotyphodium* endophytes show no outward signs of infection. Mycelium is usually found in all above ground parts of the plant but is most concentrated in the leaf sheaths and seeds. The mycelium is intercellular in the grass, seldom branched and nutrients from the plant are absorbed through the fungal cell wall. The fungus does not sporulate within or on the grass and so its only means of propagation is through mycelium in the seed. When infected seed germinates mycelium grows into the meristematic region of the seedling so that usually all tillers in the plant become infected and most or all seeds produced by the plant also become infected.

Mycelium of *Epichloe* endophytes is also intercellular within the grass but when flowering commences the mycelium emerges from the plant and surrounds the developing inflorescence preventing its emergence and so no seed is produced. This condition is known as Choke disease. Conidia are formed on the mycelial web and later perithecia are produced. Infection of endophyte-free plants is by means of ascospores. Some grasses infected with *Epichloe* such as *Dactylis glomerata* L. never set seed whereas other grasses such as *Festuca rubra* L. seldom have mycelium emerge from the plant and the fungus is propagated through the seed as with *Neotyphodium*. Environmental conditions are thought to influence emergence of mycelium at flowering, high levels of nitrogen discouraging choke disease (Sun & al., 1990).

Grass endophytes have only been studied intensively over the past 20 years. The reasons for this are given in the next section.

Economic importance of grass endophytes

An endophytic seed-borne fungus was first described in the grass darnel (*Lolium temulentum* L.) a century ago by Vogl (1898)

and in the following year mycelium was found in seeds of several other species of *Lolium* (Guerin, 1899). Darnel is also known as tares and the seed from this plant has a reputation dating back to biblical times for being poisonous. Early in the 20th century there were reports of endophyte-infected grasses being toxic to animals (Kobert, 1906; Henry, 1911). Pioneering and detailed research by Rivas & Zanolli (1909) in South America implicated an endophytic fungus in the grass *Festuca hieronymi* Hackel as being the cause of toxicosis in farm animals. Unfortunately, this important research was published in an obscure portfolio which was overlooked until recently and so the linking of endophytes in grasses with toxic effects in animals was not rediscovered until many years later. This was unfortunate because there have been many reports this century of grazing animals suffering toxicoses after eating some species of grasses which we now know or suspect are caused by toxins produced by endophytes (Gilruth, 1906; Steyn, 1933).

Bacon & al. (1977) were the first to show that fescue toxicosis only occurred in cattle which ate tall fescue (*Festuca arundinacea* Schreb.) infected with the endophyte *Neotyphodium coenophialum* (Morgan-Jones & Gams) Glenn & al. Subsequently Fletcher & Harvey (1981) showed that ryegrass staggers was caused by animals eating perennial ryegrass (*Lolium perenne* L.) infected with the endophyte *Neotyphodium lolii* (Latch, Christensen & Samuels) Glenn & al. The economic importance of these two toxicoses is great and it has been estimated that fescue toxicosis costs North American beef producers \$ 600 million each year (Hoveland, 1993). Intensive research on the two endophytes which cause these disorders of animals was begun at this time with a view to solving the toxicity problem.

Beneficial effects of endophytes

Endophyte-free (E-) tall fescue and perennial ryegrass plants can be found in their native habitat and in many pastures. Hence when it was shown that animal toxicoses only occurred when these two grasses were infected with endophytes the initial reaction of agronomists and farmers was to sow experimental plots and pastures with seed which was free of endophyte. Fields could be sown with seed harvested from E- crops or with endophyte-infected (E+) seed in which the endophyte had died. Death of the endophyte takes place when seed is stored for 1-2 years at room temperatures which are warm and humid whereas the embryo of the seed remains viable. The endophyte can also be killed by soaking seed in systemic fungicides (Latch & Christensen, 1982). When experimental E+ and E- ryegrass swards were established in New Zealand the animals which grazed the E+ swards developed ryegrass staggers while the animals on E-

swards were unaffected. However, many of the E⁻ plants subsequently died whereas the E⁺ plants remained healthy (Prestige & al., 1982).

A similar situation occurred in the USA. The incidence of E⁺ tall fescue in pastures in the southwestern states of the USA was found to average 58% (Shelby & Dalrymple, 1987) and so the sowing of E⁻ tall fescue pastures was undertaken by farmers. However in many cases E⁻ pastures did not persist. Unless grazing of E⁻ pastures was well managed the grass died and the E⁻ tall fescue plants were often replaced in the sward with E⁺ plants which had grown from seed buried in the soil or had survived from an incomplete kill of plants in the previous pasture (Shelby & Dalrymple, 1993).

These experiences indicated that the endophyte had a beneficial effect on plant persistence and so other ways of controlling these animal toxicity problems were required. An explanation as to how endophytes may be beneficial to plants was needed and so began a large research effort to study the relationship of grass and fungus.

Effects on grasses

Survival of the fungus depends upon the plant remaining alive. Any assistance the fungus can give to plant survival will ensure its own survival. Thus one has the basis for mutualism between fungus and plant. Endophytic fungi are able to synthesise a wide range of biologically active compounds (Siegel & al., 1990) which influence both the growth and persistence of the host plant. Alkaloids produced by the fungus have been most studied because some have been shown to be toxic to animals, insects and nematodes. The fact that E⁺ grasses are common in the wild and in pastures of some countries attests to the success of this mutualistic relationship between grass and endophyte.

Effects on insects

The death of ryegrass plants in the New Zealand ryegrass staggers trial mentioned above was caused by larvae of an insect, Argentine stem weevil (*Listronotus bonariensis* Kuschel), which burrow into the base of grass tillers and kill them. Peramine is synthesised in E⁺ ryegrass plants (Rowan & al., 1986). The presence of this alkaloid deters adult weevils from feeding on the grass and so eggs are rarely laid on E⁺ grasses (Rowan & Gaynor, 1986). Hence larvae are seldom present in E⁺ ryegrass tillers unless they have moved there from non-infected plants. Many insects are deterred from feeding, or are restricted in growth or killed when they eat E⁺ grasses (Latch, 1993; Popay & Rowan, 1994). The toxins involved and the effects they have on insects have been reviewed by Rowan & Latch (1994). In New

Zealand the majority of ryegrass plants in pastures are infected with endophyte. If seed with a low incidence of endophyte is sown then within a few years the majority of surviving plants will be infected. Spread of endophyte from infected to non-infected plants cannot take place so the apparent increase in E+ ryegrass plants is due to the killing of the E- plants in the population by Argentine stem weevil larvae.

Protection from drought stress

Death of E- tall fescue plants in some regions of the south western states of the USA does not appear to be due to insect predation. Read & Camp (1986) reported that E+ stands of tall fescue averaged 4% bare area whereas E- stands had 54% bare area. This followed a drier than normal summer in east Texas. Forage dry matter yields were 55% higher in the E+ pastures. Other reports on the lack of survival of E- tall fescue pastures followed. Bouton & al. (1993) compared yield and stand survival of four tall fescue cultivars grown at three locations in Georgia. They found that the E+ plants survived better than the E- plants at the two locations which had the greatest summer drought conditions. West & al. (1993) also concluded that E+ plants survived better than E- plants in non-irrigated plots whereas there was no difference in survival in irrigated stands.

The reasons for the enhanced tolerance to drought of E+ tall fescue have been investigated and it appears that many factors could be involved. Buck & al. (1997) have found that in some genotypes of droughted tall fescue plants the stoma closed faster in E+ leaves than in E- leaves. There is an interaction here between the grass and the endophyte and hence E+ grasses may differ in their drought tolerance. Plant genotype appears to play an important role in many endophyte/grass relationships. An example of this is provided by Belesky & al. (1987) and Richardson & al. (1993) who found that E+ tall fescue plants have lower stomatal conductance and lower rates of photosynthesis than E- plants but these differences have not always been consistent and have varied with the plant genotype and the environment. Consideration was not given as to whether the strain of endophyte in the plant could also be affecting these differences. The linking of plant osmotic adjustment and drought tolerance has been demonstrated by West & al. (1990). They showed that tillers of E+ tall fescue had high osmotic adjustment and they proposed that the vegetative growing points of these infected tillers would survive better under drought conditions than E- tillers. However, in recent studies Buck & al. (1997) concluded that endophyte enhanced tiller survival is probably due more to postponement rather than tolerance to desiccation of the growing zone. Experiments

by Richardson & al. (1991) suggest the reason for this was that E+ tall fescue had greater concentrations of fructose and glucose than E- plants when grown under drought stress. Leaf rolling during drought stress occurs with some grasses but Elmi & West (1995) and White & al. (1992) found that endophyte did not influence this.

In addition to the physiological factors just discussed there are other factors which may influence drought tolerance of E+ grasses. Richardson & al. (1990) observed that the roots of drought stressed E+ tall fescues grew faster and deeper into the soil than E- plants. It has also been shown that E+ tall fescues are resistant to the predation of several species of nematodes (Bernard & al., 1997) and so the roots of E+ plants could access moisture from deeper in the soil and be in better condition to take up the moisture than would E- plants.

The strain of endophyte species present in the plant may also play a role in drought tolerance. The phytohormones abscisic acid and indole acetic acid (IAA) are synthesized by *N. coenophialum* (Bunyard & McInnis, 1991; De Battista & al., 1990), the quantities produced depending upon the fungus strain. These hormones regulate stomatal conductance (Lachno & Baker, 1986) and so the apparent difference in drought tolerance by different plant genotypes may be due both to the plant and to the strain of endophyte it contains.

Protection from plant disease

There are a few instances where endophytes have been shown to protect their host grasses from plant diseases. Shimanuki (1987) was the first to record that *Phleum pratense* L. plants infected with *Epichloe typhina* were resistant to the leafspot fungus *Cladosporium phlei* (Gregory) de Vries. Since that time tall fescue seedlings infected with *N. coenophialum* have been shown to be more resistant to *Rhizoctonia* root rots than E- seedlings (Gwinn & Gavin, 1992), fine fescues infected with *Epichloe* species more resistant to *Sclerotinia homoeocarpa* Bennett (Clarke & al., 1994) and meadow fescue (*Festuca pratensis* Huds.) infected with *N. uncinatum* Gams, Petrini & Schmidt more resistant to attack by *Drechslera sorokiniana* (Sacc.) Sub. & Jain and *Rhizoctonia cerealis* Van der Hoeven (Schmidt, 1994) than E- plants. However, Funk & al. (1994) give one instance where an E+ turf grass was more susceptible to *Pythium* blight than E- plants. In vitro tests with cultures of pathogens and endophytes have shown that many pathogens are only inhibited in growth by particular strains of endophyte species (Siegel & Latch, 1991; Christensen, 1996). Hence, it is possible that if plants are infected with a strain of endophyte known to inhibit the growth of particular pathogens then a greater range of plant diseases may be affected.

Effect on plant growth and competition

Endophytes in grasses can affect the growth and persistence of their host in many other ways. They can influence the yield of grass. In one trial clones of E+ ryegrasses grown in the equivalent of full sunlight in a phytotron produced more herbage than did the same clones when they were not infected with endophyte (Latch & al., 1985). However, trials by other experimenters showed that increased plant growth does not always result from endophyte infection. The importance of environmental factors on the interaction of host and endophyte was demonstrated by Clay (1987) and Marks & Clay (1989) who found that E+ plants growing under full sunlight produced more herbage than E- plants but when the light intensity was reduced to 50% or 25% of full sunlight the E- plants outgrew the E+. The effect of plant nutrition on the interaction of endophyte and plant has not been explored to any great degree but there is some evidence (Arachevaleta & al., 1989) that in soils which are deficient in nitrogen E+ tall fescues utilize nitrogen from the soil better than E- fescues. Glutamine synthetase is the enzyme responsible for nitrogen utilization and it is present in greater quantities in E+ than in E- plants (Lyons & al., 1990).

The ability of *N. coenophialum* to synthesise phytohormones has already been mentioned. Indole acetic acid is involved in cell elongation and plant tillering, the concentration affecting the degree to which this occurs. Plants also produce IAA and so the effect on plant growth is influenced by the genotypes of both host plant and endophyte. The ability to tiller profusely is of great advantage to grass survival. Both tillering and root production are reduced when grasses are flowering because of the controlling influence of the inflorescence. When grasses are prevented from flowering, such as when they are infected with *Epichloe* endophytes, there is no reduction in tillering. At this stage the endophyte can be regarded as pathogenic because the grass produces no seed but it can also be regarded as beneficial because tillering is increased. Ecological studies on *Agrostis* species by Bradshaw (1959) and Watkins (1987) showed that infection by *Epichloe* conferred a positive advantage to its grass host when growing in competition with an E- grass of the same species. They found that endophyte-infected *Agrostis* species predominated in swards that had been undisturbed for many years. Successful re-seeding of grasses in undisturbed grass swards is rare because of the dense nature of the sward (G. Edwards, pers. comm.). Hence the prevention of flowering by *Epichloe* mycelium does not disadvantage the infected grass and is in fact beneficial because the increased tillering of infected plants increases their competitiveness. Thus in situations like this endophyte-infected grasses reduce the diversity of plant species in the field by displacing uninfected species.

Animal disorders

The benefits that endophytes confer to their host grasses discussed so far are also beneficial to pastoral farmers because they result in enhanced plant growth and persistence. However, one aspect of grass/endophyte mutualism which is not appreciated by farmers is the effect that most E+ grasses have on the health and production of animals and on the palatability of grass.

Fescue toxicosis is one example of a disorder of animals caused by an endophyte. During the warmer parts of the year animals grazing E+ tall fescue gain little or no body weight, they develop fat necrosis and females produce less milk and have reduced fertility when compared with animals grazing E- tall fescue (Steudeman & Thompson, 1993). In cold weather animals eating E+ tall fescue may develop gangrene of the feet and tail. The alkaloid ergovaline is believed to be responsible for many of these conditions.

Ryegrass staggers is another example of animal toxicity. It is a neuromuscular disorder which occurs in the warmer months of the year and is caused by animals eating E+ perennial ryegrass. The toxin is an alkaloid called lolitrem which is synthesised by the endophyte *N. lolii* (Gallagher & al., 1984). In severe cases animals can die from dehydration or from drowning when affected animals undergo spasms while drinking from ponds or streams.

Narcosis symptoms are induced in animals which eat E+ *Stipa robusta* (Vasey) Scribner or *Stipa inebrians* (Vasey) Keng. Animals recover after several days but they refuse to eat that species of grass again (Petroski & al., 1992; Bruehl & al., 1994).

Such defences of endophyte-infected grasses are of benefit to plant survival but not to animal welfare. Farmers benefit, however, from the effects that E+ grasses have on small animals and birds. Birds show a preference for tall fescue grass and seed which is free from endophyte-infection (Conover & Messmer, 1996; Madej & Clay, 1991) and hence the loss of seed from crops is reduced when the grass is infected with endophyte. Pelton & al. (1991) have observed that small animals such as mice, voles and shrews are found more frequently in E- tall fescue fields than in E+ fields. These animals while doing little damage to pastures themselves are the prey of stoats and weasels which are carriers of tuberculosis and can be a source of infection of this disease to farm animals.

Strains of endophytes

Within species of endophytes there are many strains. Reference has already been made to the variation between strains in their ability to synthesise phytohormones or inhibit colony growth of pa-

thogens. Strains of endophytes have been shown to differ in their ability to synthesise compounds including the alkaloids which affect animal health and insect deterrence (Lane & al., 1997; Hill & al., 1991; Latch & Tapper, 1988; Jones & al., 1997). Early agronomic studies comparing herbage production from different species and cultivars of grasses did not take into account the quite considerable effects that endophytes may have on their grass hosts. It is now becoming apparent that the strain of endophyte present in the grass is of importance because strains differ in their influence on the growth, persistence and toxicity of the grass. Thus both the genotype of the grass as well as the genotype of the endophyte must be considered when assessing the value of future grass cultivars.

Artificial infection of endophytes

Neotyphodium and *Epichloe* endophytes can be cultured and transferred from one grass to another. This can be done through the inoculation of seedlings (Latch & Christensen, 1985), callus culture (Johnson & al., 1986), plantlets derived from meristems (O'Sullivan & Latch, 1993) or directly into tillers (Ravel & al., 1994). Selected desirable strains of endophytes can be infected into new grass cultivars so that their growth and persistence may be improved and their toxicity to animals reduced.

Endophytes in one grass genus can be infected into grasses of closely related genera and although the transfer is initially successful, in many instances the endophyte will most likely gradually disappear from its new host. In a few cases the endophyte becomes pathogenic in these new combinations (Koga & al., 1993) and the grass dies. Transfer of endophytes within grass species is much more successful and the percentage of plants which lose their new endophyte is very low. Christensen (1997) in a short review lists factors influencing endophyte compatibility with artificially infected grasses.

Seed transmission of endophytes

In nature it often happens that a small percentage of seed produced by endophyte-infected grasses does not contain mycelium (Welty & al., 1994). They observed that some tall fescue plants in seed crops had tillers which were free of endophyte and all seed set from these tillers was endophyte-free. Endophyte-free seed may also be produced by some plants which have been artificially infected with endophytes. Wilson & Easton (1997) found that mycelium sometimes fails to penetrate the meristem of branches of panicles, or having penetrated, fails to grow out into the resulting branch. How-

ever, I have found that when an endophyte is inoculated into grasses of the same species as that from which it was originally isolated then, in the majority of cases, seed transmission is 100% or very close to this figure. Plant genotype is of importance and this has been shown by Easton & Latch (unpublished) who found that a minority of individual plants of some ryegrass cultivars when artificially infected with endophytes had low transmission of mycelium in seed. If these plants can be identified and rogued then the overall incidence of endophyte mycelium in seed from the remaining plants in subsequent seed crops should be very high. The economic use of desirable endophytes in grasses depends upon a high transmission of the endophyte in seed.

The relationship of host and endophyte is a very intimate one and so when new strains of endophytes are infected into grasses the stability of the new combinations must be thoroughly tested.

When E+ seed is stored the mycelium does not remain viable as long as the seed does. Endophyte strains differ in their ability to retain their viability in storage, some losing their viability very quickly (Latch, unpublished). The reason for this is unknown but would be a profitable field of study because retention of endophyte viability in seed during storage is crucial to economic exploitation of new combinations of endophyte and grass.

Practical use of selected endophytes

Strains of endophytes have been found in nature which produce little or none of the alkaloids responsible for animal toxicoses (Latch & Tapper, 1988). Thus, there is an opportunity to infect these desirable strains into grass cultivars and avoid the animal health problems associated with the toxins. The amount of alkaloid produced by an endophyte is influenced by the host grass. Latch (1994) reported that ryegrass plants of the same cultivar when infected with the one strain of endophyte had a ten-fold variation between plants in the amount of ergovaline synthesised. Thus a strain of endophyte which produces low levels of toxin in one plant may produce high levels in another. Hence it is important that the strain of endophyte selected for infection into plants is incapable of synthesising the compound(s) responsible for animal toxicoses. Practical application of a strain of *N. lolii* which is incapable of producing lolitrem has been exploited in New Zealand by artificially infecting it into a cultivar of ryegrass. This cultivar has been available to farmers since 1992 and there have been no reports of ryegrass staggers in animals which graze it. Unfortunately this strain of endophyte produces a small quantity of ergovaline in ryegrass and this alkaloid is known to induce symptoms of heat stress in animals during hot weather.

Further improved strains which produce neither lolitrem nor ergovaline but which do produce the insect toxin peramine will be available in many ryegrass cultivars shortly.

A method of producing cultivars of grasses which may have reduced toxicity to animals was investigated by Agee & al. (1994). They crossed E+ tall fescue plants which produced different amounts of ergovaline. By selecting plants which had the lowest levels of ergovaline they postulated that eventually a line of plants could be developed as a cultivar which produced little ergovaline. The disadvantages of this method are that the crossing process takes many years and the plants still produce low levels of toxin.

Molecular biology techniques may be useful in modifying strains of endophytes. Murray & al. (1992) transformed a hybrid endophyte of perennial ryegrass, distinct from *A. lolii*, by using linear and circular forms of pAN7-1, a hygromycin (*hph*) resistant plasmid. Whereas 80% of the linear transformants were stable only 25% of the circular transformants retained hygromycin resistance on further culturing. Integration of pAN7-1 into the genome was confirmed by Southern blotting. The β -glucuronidase (GUS) gene, *uidA*, was also introduced into the fungus by co-transformation of pNOM-2 with pAN7-1. These transformed endophytes were then infected into perennial ryegrass seedlings and GUS activity confirmed in the leaf sheaths of mature plants. Tsai & al. (1992) used electroporation to introduce hygromycin resistance into *N. coenophialum*. This technique gives a much lower transformation frequency than that obtained by Murray & al. (1992) but has the advantage that once the protoplasts have been prepared it involves less manipulation. Thus it is now possible to insert desirable genes into grasses by way of their endophytes and so genes such as the Bt and protease inhibitor genes could be introduced into endophytes to control insects which feed on the grass. As more is known about the synthetic pathways of alkaloids in grasses it should also be possible to disrupt the genes in these pathways and so prevent the production of toxins which affect animal health. This technology opens exciting possibilities (Schardl, 1994) but it will be some years before it is put into practice.

Conclusion

The study of grass endophytes is proving to be a fascinating one. It has been revealed that endophytes have a remarkable influence on their host through their ability to synthesise compounds which affect not only the physiology of the grass but also the pests and diseases which can attack it. A growing awareness of the profound effects that endophytes have on plant competitiveness, growth and persistence is helping scientists understand the ecology of natural grass-

lands. For agriculturalists, an understanding of the role that endophytes play in pasture production and persistence and in animal health has lead to solutions for controlling the disorders that E+ grasses may produce in animals. Where it is not possible to replace the toxic E+ grasses our knowledge of which parts of the plant are most toxic and at which times of the year toxin levels are highest enables farmers to use grazing management strategies which will reduce the amount of toxin ingested by animals.

It is under conditions which are stressful to the plant that the benefits of endophyte infection are most noticeable. In those parts of the world where endophytes do not appear to benefit grass production or survival then the use of E- grasses in pastures is warranted. However in environments where endophytes are beneficial to their host grasses it is desirable to sow E+ cultivars infected with strains of endophytes which synthesise compounds facilitating plant growth and persistence but not the production of toxins causing disorders of animals.

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