The physiological basis of containerised tree seedling 'transplant shock': a review

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Summary

Tree seedlings are planted on sites of widely differing climatic, edaphic and vegetative characteristics. Seedling transplant shock, defined as seedling mortality or impaired growth soon after planting, has been reported across this spectrum of planting conditions. Thus, transplant shock is used to describe a phenomenon that embraces many distinct physiological responses to stress. This review lists and discusses the potential sources of transplant shock for containerised tree seedlings and suggests options for minimising its detrimental effects for a range of specific causes. Through an understanding of the physiological basis underlying transplant shock under a given set of conditions, it may be possible to eliminate, or at least minimise, the effects of transplant shock on containerised tree seedlings soon after planting.

Keywords: forest nurseries; planting stock; transplanting; physiology; shock; competition; drought; frost; nutrition; photoinhibition; pigments; root:shoot ratio; reviews

Introduction

Transplant shock, also referred to as transplant stress or planting check, is used to describe the negative effects on growth and survival when nursery-raised stock is planted into a new environment. Transplant shock is expressed through a range of symptoms that include a decreased growth rate of newly planted seedlings compared to naturally regenerating seedlings of the same age, and leaf abscission and mortality under severe conditions (Reitveld 1989). Transplant shock is associated also with acclimatisation of seedlings to the new environmental conditions.

The sites to which seedlings are transplanted can encompass a wide range of climatic and edaphic conditions. Thus transplant shock is often used to describe a suite of visual or growth responses to plant stress that are related to distinct physiological mechanisms or processes. The description of these various processes using a single term is therefore, at best, ambiguous. The definition of transplant shock is further complicated by the wide range of physical, nutritional and physiological states of seedlings that it is attributed to. These states, and the way they interact with the condition at the planting site, predispose seedlings to specific forms of plant stress.

This paper addresses the physiological basis of tree seedling transplant shock in the context of possible factors that underlie its cause. These factors are separated into three categories: (a) within-plant characteristics; (b) abiotic stress factors; and (c) interaction with the surrounding environment.

Within-plant characteristics

Acclimatisation between the nursery and the field

Tree seedlings acclimatise to the growing environment in the nursery. If field conditions differ from those in the nursery, the transplanted seedling will be stressed as acclimatisation occurs over several days or weeks. Many plant stresses have a negative effect on photosynthesis. Thus strategies for dealing with light absorption under conditions of decreased photosynthetic activity are crucially important to seedlings suddenly exposed to new environmental conditions. The occurrence of decreased photosynthetic efficiency is termed photoinhibition. This may arise directly due to sudden increases in irradiance, or indirectly through a stress that limits photosynthesis and induces conditions of excess light absorption, e.g. low temperature, water-logging or drought. Low temperature limits photosynthesis by slowing dark reactions (Havaux 1995; Stitt and Hurry 2002). Water-logging and drought restrict water uptake (Bradford and Hsaio 1982; Munns *et al.* 1983) and limit photosynthesis primarily through stomatal closure (Chaves 1991).

Photoinhibition is defined as a sustained reduction in the efficiency of photosystem II (Long *et al.* 1994) and occurs whenever the absorption of light energy exceeds its utilisation (Huner *et al.* 1993). Various physiological processes are available in plants to dissipate this excess energy. Three of these processes are the xanthophyll cycle (Close *et al.* 2003a), the capacity of which is proportional to the size of the xanthophyll cycle pool (Adams and Barker 1998), photorespiration, and the water-water cycle (see Niyogi 1999). If their capacity for dissipating excess energy is exceeded, highly reactive and damaging oxygen and chlorophyll

radicals are formed (Asada 1992; Foyer *et al.* 1994). Scavenging compounds and enzyme systems quench these radicals but their capacity can also be exceeded. Damage to chlorophylls, carotenoids and lipid bilayers results in photobleaching or photodamage to plant tissues (Wise and Naylor 1987). If severe, leaf death and abscission and seedling mortality can result (Close *et al.* 1999, 2000).

A fourth means of photoprotection is anthocyanin. This pigment is synthesised immediately below the epidermis in *Eucalyptus globulus* and *E. nitens* (Close 2001; Close *et al.* 2000, 2001b), *Pinus sylvestris* (Nozzolillo *et al.* 1989) and *P. banksiana* (Krol *et al.* 1995) seedlings. It is hypothesised that anthocyanin alleviates photoinhibition by absorption of light between 400 and 590 nm (Pietrini and Massacci 1998; Close and Beadle 2003b, 2004a). The accumulation of foliar anthocyanin has been proposed to be an indicator of hardiness to low temperature in *E. nitens* seedlings (Close *et al.* 2004a).

The acclimatisation condition at planting will depend to a large extent on the difference between the nursery and planting environments. Some acclimatisation is always required, as seedlings are grown at high densities and self shade in the nursery, resulting in some foliage being shade adapted. For example, nursery-grown seedlings of eastern hemlock (*Tsuga canadensis*) had survival of 58 and 100% after transplanting from shaded to fully exposed or shaded planting sites, respectively (Mohammed and Parker 1999).

The potential capacity of a seedling to acclimatise to field conditions is also important (Close *et al.* 2001a). Different species and sub-populations within species have different capacities to acclimatise to a large increase in irradiance (Battaglia *et al.* 1996; Tognetti *et al.* 1998). For example, *E. nitens* seedlings have higher concentrations of anthocyanin and carotenoids than *E. globulus* seedlings raised under identical conditions and therefore require less acclimatisation after planting and exposure to high light (Close *et al.* 2000, 2002). Similar differences exist amongst conifers. Sun scald or photodamage is a significant cause of mortality in seedlings of *Tsuga canadensis*, *T. heterophylla* and *Abies amabilis* (Tucker and Emmingham 1977; Tucker *et al.* 1987) following transplanting. However, rapid acclimatisation of pre-existing foliage to the higher light environments associated with field conditions has been reported for *Picea abies* (Spunda *et al.* 1993) and *Picea glauca* (Leiffers *et al.* 1993). Acclimatisation to the prevailing light condition may be differentiated at the species and subspecies level through the activity of the xanthophyll cycle (Adams *et al.* 1994).

One method of minimising the period and extent of acclimatisation after planting is to carefully match species to site characteristics. This practice has been the focus of much research (Saunders *et al.* 1984; Booth *et al.* 1988, 1989; Booth and Pryor 1991) and has been adopted by the forestry industry. The importance of the state of acclimatisation of a seedling at planting is also recognised in the forest industry. Outdoor nursery areas in conjunction with the withholding of nutrients and/or water are commonly used to 'harden off' seedlings (Colombo 1986; Gebre and Kuhns 1991; Anderson and Helms 1994). The withholding of nutrients is usually an effective means of hardening for low field temperatures. For example, the risk of cold-induced photodamage was minimised when seedlings raised in a mild environment were deprived of N

in the nursery (Close *et al.* 2000). However, if exposure to low temperature before planting has occurred, N deprivation may not be required as seedlings may already be hardened to cold-induced photoinhibition (Close *et al.* 2001a,b).

Nutritional status

Fertiliser application using water-soluble nutrients via irrigation systems ('fertigation') is used as a management tool to control and adjust seedling growth rate in the nursery (Close and Beadle 2004a). Thus seedlings can vary to a large degree in their micro- and macro-nutrient concentrations (Larsen *et al.* 1988). Conversely, toxicities and deficiencies can occur due to inappropriate nutrient application or imbalance of applied nutrients. Macro-nutrient deficiencies are the most common and are a major source of transplant shock.

Nursery managers use macronutrients to manage seedling growth and to meet a particular seedling specification. Foliar nitrogen has been shown to correlate strongly with seedling growth after planting (Carlson 1986; Larsen *et al.* 1988; Thaler and Pages 1996; Close *et al.* 2003b, 2005). Seedlings deficient in N put their available resources into root growth, to acquire N, at the expense of shoot growth. Recent evidence has indicated the importance of N stored in foliage, and its retranslocation, for new growth (Close 2001; Warren and Adams 2001; Close and Beadle 2003a, 2004b). Internal recycling of nutrients from foliage has been shown to supply up to 100% of nutrients for new growth in seedlings soon after planting (Folk and Grossnickle 2000).

Sampling for foliar nutrient analysis is widely practised and indicates the necessity for corrective nutrient application during the seedling production period. Trials of nutrient application methods for nurseries under well-defined environmental conditions (Close *et al.* 2003c, 2004b, 2005) and using potting mixes that affect the leaching (Geraldson 1996) and draw-down (Bragg and Whiteley 1995) of nutrients have provided useful information. For example seedlings at nurseries in regions of high temperature and rainfall need higher levels of nutrient application for a given level of uptake, as more nutrient remains in solution and leaches out of the potting mix. Seedlings in potting mixes with higher air-filled porosity and higher microbial populations also need higher nutrient application for a given level of uptake, as leaching and draw-down are proportionately greater.

Nutrient/carbohydrate reserves and biomass partitioning

Carbohydrate and nutrient reserves in seedlings at planting need to be above a critical level to ensure that new growth occurs: this level may be species dependent and vary with site conditions (Balneaves and Fredric 1983; Balneaves *et al.* 1985; Lauer 1987; Jinks and Kerr 1999; South and Mitchell 1999). Levels of carbohydrate and nutrient reserve are related to seedling size (Ritchie 1982). For example, the larger of two *P. banksiana* stock types of otherwise similar genetic origin and age had greater survival and growth relative to the smaller stock type (Mohammed *et al.* 1998). In the same study, larger amounts of available, retranslocatable nutrient were associated with higher photosynthetic rates (Mohammed *et al.* 1998). Adequate carbohydrate reserves are essential also under conditions where photosynthesis is restricted but resources are still required for maintenance

respiration and to support new leaf development where stress (e.g. severe drought, frost or browsing) has led to leaf loss after planting.

Low shoot:root ratio and high root regeneration capacity (characterised by a high number of root tip apices) are desirable for maximising new growth after planting. However, the shoot:root ratio is relatively high after nursery production in containers and this restricts acquisition of sufficient nutrients and water to support shoot growth after planting (Ledig 1983; Reitveld 1989; Close 2001). For example, growth of *Pinus taeda* seedlings after planting was strongly negatively correlated with shoot:root ratio at planting (Larsen *et al.* 1988). The physiological basis of this effect has been investigated using just-transplanted, non-water-stressed *Picea mariana* seedlings. The seedlings had decreased levels of all foliar macro- and some micro-nutrients, total amino acids and sucrose relative to non-transplanted controls (Young *et al.* 1999). These results are consistent with those in recently-transplanted *Eucalyptus* seedlings (Close 2001; Close and Beadle 2004a) and are indicative of retranslocation of mobile nutrients to enable new root growth.

Container depth has been found to better correlate with seedling growth after planting than container volume and many other pre-planting seedling specifications (Close *et al.* 2003b). Deeper containers do not necessarily decrease shoot:root ratio but affect root architecture by increasing the initiation of primary roots in the container (Nelson 1996). Thus the soil mass initially occupied by roots increases with increasing container depth.

Large seedling size ensures an adequate carbohydrate and nutrient reserve after planting (South and Mitchell 1999). However, this should not be driven by an increased shoot:root ratio which can be detrimental to successful establishment (Larsen *et al.* 1988). Seedling production in larger plugs (i.e. ≥ 85 cf. 50 cm^3) with adequate, but not excessive, fertiliser application, and minimising the holding period in the nursery to keep down shoot:root ratio, may be desirable. Avoidance of shallow containers will ensure poor root architecture does not limit seedling growth after planting.

Abiotic/environmental stress

Drought

Drought-induced stress is the most widely studied and perhaps the most common cause of transplant shock in tree seedlings (Jarvis and Jarvis 1963; Burdett *et al.* 1983, 1984; Grossnickle 1988). Seedlings often become water stressed soon after planting, as the soil volume accessed by roots of a naturally established seedling is more than ten-fold that of a transplanted seedling of the same shoot size (Burdett 1990). Drought stress following transplanting is further exacerbated by poor acclimatisation to the field environment (Rowe 1964). In the nursery, seedlings are within relatively close proximity to one another, sheltered from wind and watered frequently. Under such conditions leaves of high area:mass ratio and seedlings of high shoot:root ratio are formed which are not well suited to maintaining a favourable water balance in field environments. A low shoot:root ratio leads to a better balance between root water acquisition and shoot water loss following transplanting (Ledig 1983) and a low leaf area:weight ratio minimises stomatal water loss (Wright *et al.* 2001).

Leaves have physiological mechanisms that provide adaptation to drought. Maintenance of leaf turgor, that is required for many growth-related processes, can be achieved through changes in osmotic potential or tissue elasticity (Tyree and Jarvis 1982). Adjustment in either osmotic potential (e.g. Anderson and Helms 1994), or cell wall elasticity (e.g. Bowman and Roberts 1985), or a combination of the two (e.g. White *et al.* 1996) occurs in response to drought stress. Osmotic adjustment, by decreasing the osmotic potential of the cells, increases water retention under dehydrating conditions. This is achieved using organic solutes, termed compatible solutes due to their compatible nature with the structure and function of other cellular macromolecules. Sugars and free amino acids contributed to osmotic adjustment in *Picea mariana* seedlings during development of drought tolerance (Tan *et al.* 1992). Increased cell wall elasticity involves increases in hemicellulose and decreases in lignin and cell wall pectin in *P. glauca* seedlings subjected to drought conditions (Zwiazek 1991).

A watering regime slightly restricting water availability to seedlings may induce morphological and physiological characteristics conferring drought tolerance (Bacon and Bachelard 1978). This may be effected by plant endogenous growth substances. Drought-conditioning, through either irrigation cycling in the nursery or root pruning in open-rooted stock, significantly reduced levels of gibberellin and cytokinen activity, increased inhibitor levels, and had no effect on auxin activity in *Pinus caribaea* seedlings (Bacon and Bachelard 1979). An induced water limitation decreased leaf mass:area ratio which was associated with drought tolerance in *Picea sitchensis* (Hellkvist *et al.* 1974). Droughting in the nursery decreased osmotic potential in seedlings of *Eucalyptus camaldulensis*, *E. tereticornis*, *E. viminalis* and *E. grandis* (Lemcoff *et al.* 1994) and decreased osmotic potential and increased cell wall elasticity in *P. mariana* seedlings that led to the development of drought tolerance after planting (Colombo 1986).

Frost

Tree seedlings planted into cold environments are susceptible to frost damage for a number of reasons. Firstly, the seedlings may not be acclimatised to the low temperatures experienced after planting. Secondly, young, recently developed foliage often has a high water content and relatively large-celled leaves with a low osmotic concentration, characteristics that are associated with a high susceptibility to frost. Thirdly, cold air stratification and pooling of cold air close to ground-level expose seedlings to extremely low temperatures. Fourthly, cleared forest sites attain minimum temperatures below adjacent forested areas due to the loss of infra-red radiation to clear night skies (Nunez and Bowman 1986). In addition, the leaf temperature of exposed leaves at night may be lower than the air temperature due to radiative cooling (Jordan and Smith 1995). Nevertheless, tree seedlings often adjust to the prevailing site conditions. This is because tree seedlings acclimatise, or 'harden', to frost. Unusually early or late frosts can cause serious frost injury, as seedlings may not be hardened. Further, hardening occurs within certain genetic constraints. For example, *E. globulus* has a lower frost tolerance than *E. nitens* under identical environmental conditions, and this is a factor in

its planting distribution (Hallam *et al.* 1989; Close *et al.* 2000; Davidson *et al.* 2004). *Eucalyptus nitens* populations from distinct geographic origins also differ in their susceptibility to frost (Raymond *et al.* 1992a,b).

Low, non-freezing temperatures trigger increased frost tolerance or hardiness. The physiology of frost tolerance involves a general relationship where hardiness is correlated with increased concentrations of soluble sugars and other compatible solutes (Ögren *et al.* 1997; Wanner and Junttila 1999) and increased cellular membrane stability via changed lipid composition (Thomashaw 1999). The frost tolerance of *Pinus radiata* (D. Don) increases in a curvilinear fashion as low, but above-freezing temperatures decrease. Hardening occurred at temperatures below, and dehardening at temperatures above, 9.5ºC. The balance between the two processes determines the development of frost hardiness (Greer *et al.* 2000).

Logging minimum temperatures in the nursery can provide an initial indication of potential frost hardiness. Many nurseries are situated at low altitudes on mild sites that maximise the early growth of seedlings. In this case, an intermediate holding area at higher altitude may be beneficial before planting on cold sites, although in practice this may be difficult to manage. Matching the hardening potential of species to site conditions is essential and widely practised (Tibbits *et al.* 1997). Tree guards can mitigate frost effects by excluding cold air flow at night and by trapping warm air during the day.

Mechanical damage

Mechanical stress, predominantly caused by wind but also by snow, ice or rain, can lead to stem breakage after planting. In the nursery, seedlings protect each other from wind. In addition, nurseries are in sheltered locations or protected by windbreaks. Apart from lack of acclimatisation to wind, the risk of stem breakage is exacerbated if seedlings have large and broad tops, have a large height:stem diameter ratio (Essen 1994; Munishi and Chamshama 1994; Guo 1999; Peltola *et al.* 2000) or have inadequately lignified stems due to rapid growth or nutrient imbalance (Graham 1976; Turvey *et al.* 1992; Cachorro *et al.* 1993; Dell 1994; Padu 1999).

Thigmomorphogenesis is defined as 'the strain and associated physiological and morphological responses of plants to wind and other mechanical stresses' (Jaffe 1973). The few studies on thigmomorphogenesis in herbaceous annuals and tree seedlings indicate that seedlings show relatively large responses to low doses of artificial flexure or wind (Jaffe 1980; Telewski and Jaffe 1986a,b). In general, there is either decreased height growth or increased collar diameter growth or both; increased xylem production at the point of flexure; and decreased leaf area.

Seedling stems of *E. nitens* have been observed to be 'flattened' after strong winds soon after removal from the glasshouse to an outside growing area. However, they resumed their upright habit within one to two weeks after the event (Close unpublished results). Stem breakage of 7–8% of rapidly grown *E. globulus* (indicative of inadequate lignification) occurred within 4 weeks after planting during high wind events, but none thereafter (Close *et al.* 2003b). Thus, unless extreme wind, snow, hail or rain events occur, seedlings are likely to rapidly and successfully acclimatise to

environmental conditions through thigmomorphogenesis after planting.

Considerable research has been conducted by the horticultural industry on 'brushing' vegetable seedlings by passing a lowered boom across seedling tray beds set at 75% of seedling height (Latimer and Thomas 1991; Baden and Latimer 1992; Johjima *et al.* 1992; Garner and Björkman 1996) or alternatively using high-powered fans to simulate natural winds (Biddington 1986; Jeong and Lee 1990). However, use of these techniques in the forestry industry has not yet been reported. Exposure of seedlings to a naturally windy environment is an alternative method of treatment (Hunt and Jaffe 1980; Cipollini 1998). This can be a holding area at the nursery if not too sheltered, or alternatively, an exposed site. Sufficient stem lignification can be ensured by matching the utilisation of nutrients to their application (Cachorro *et al.* 1993). This will have the effect of ensuring that leaf area is not excessive, which keeps 'bushiness' down. Seedlings should not be shaded as this leads to excessive stem elongation (Ballare *et al.* 1991; Weinig and Delph 2001).

Interactions with the surrounding environment

Soil physical and nutritional conditions

Soil physical condition has a large impact on seedling growth rates soon after planting. Many studies have shown the benefits to seedling growth of decreasing soil bulk density by mounding the topsoil and/or ripping to about 0.5 m depth (e.g. Shishiachi and Adachi *et al.* 1982; Corns 1988; Minore and Weatherly 1990; Kube 1993; Farrish *et al.* 1995; Conlin and van den Driessche 1996) particularly where soils contain high clay content or hardpans and where lack of soil cultivation can decrease seedling survival (Whitman *et al.* 1997). The benefits of cultivation are due to the decreased amount of energy the seedling has to expend to extend its roots into the soil profile and acquire essential oxygen, water and nutrients (Conlin and van den Driessche 1996). Growth of *E. nitens* (Kube 1993), *P. taeda* (Scheerer *et al.* 1995), *Swietenia macrophylla* (Whitman *et al.* 1997), *Pinus rigida*, *P. nigra* and *Picea abies* (Halverson and Zisa 1982) seedlings was impaired if planted onto compacted, uncultivated compared to cultivated soils.

If soils are blocky or clumpy and seedlings are not planted carefully, poor rootball-soil contact can occur (Sands 1984; Wilson and Clark 1998), particularly if soils of high clay content shrink and crack upon drying. Coarse-textured potting media lose moisture to finer-textured or drier soils (Heiskanen and Rikala 2000). This causes air gaps to form between potting media and surrounding soil, and prevents moisture and nutrient uptake (Sands 1984). The recovery of the transplanted seedlings is a function of the rate at which new roots regenerate (Sands 1984). Root ball exposure to the soil surface often results in drought-induced mortality as the high air-filled porosity of potting mix induces rapid dehydration upon exposure to air.

Many studies have demonstrated the benefits of fertiliser application to seedlings soon after planting on infertile soils (e.g. Drechsel and Schmall 1990; Herbert 1990; Barros *et al.* 1992; Grewal *et al.* 1993; Mhando *et al.* 1993; Li *et al.* 1999). Such application can offset the need for stored reserves, increase the shoot:root ratio required at planting, and speed the onset of shoot

growth. However, nutrient applied too close to the base of seedlings can be toxic and lead to reduced growth and seedling death. Fertiliser application in a spade slit 10–15 cm down-slope of the seedling stem is recommended (Smethurst 1998).

Cultivation, mounding and sometimes ripping of soil, are now considered standard or best practice techniques for site preparation for rapid seedling growth after planting (e.g. Kube 1993). Soil variation with depth, determined with a soil auger, can indicate hardpans or clayey subsoils and thus the potential benefit of ripping. Loss of soil-root ball contact does not usually occur if soil cultivation produces a fine tilth (Sands 1984), mounds are left to settle for at least 2–3 mo and seedlings are planted with care so that the potting mix of the root ball is well covered by soil and the soil firmly surrounds the root ball (M. Lavery, Arianda Pty Ltd, Newport, Vic., July 2001, *pers. comm.*).

Competition with surrounding vegetation

Weeds often invade planting sites before, during or soon after planting. Broadleaved weeds and grasses can compete very strongly for light, water and nutrients. Grasses are particularly vigorous competitors, forming dense root mats immediately below the soil surface (Watson 1988; Harmer 1996). This can severely stress tree seedlings with small root balls which are limited in their ability to acquire water and nutrients within the soil profile (Burdett 1990) and then may become light limited if weeds grow taller than seedlings (e.g. Flint and Childs 1987; Jobidon *et al.* 1998; Wang and Wang 2000). For example, under conditions of herbaceous vegetation competition, larger *P. banksiana* seedlings had survival and collar diameter increments of 60% and 0.33 mm compared to 37% and 0.25 mm of smaller seedlings of similar genetic origin and age (Mohammed *et al.* 1998). A further detrimental effect of competing vegetation is an increase in frost severity and occurrence (Ball *et al.* 1997). *Eucalyptus pauciflora* seedlings were exposed to average minimum air temperatures 2°C higher when planted into bare soil than into a grassy ground cover (Ball *et al.* 1997). The temperature of bare soil also increases more rapidly and to a higher temperature than if covered by grass, as grass insulates the soil during the day. Thus greater frost severity and occurrence can be detrimental to seedling growth in spring and ultimately shorten the effective growing season (Ball *et al.* 1997).

Seedling size, large reserves of carbon and nutrients, and a high root:shoot ratio increase the ability of tree seedlings to compete for light, water and nutrients (Mohammed *et al.* 1998; South and Mitchell 1999). Effective weed control is essential, using knockdown and residual herbicides or mulching if practical. Mechanical scalping (removal of top few centimetres of soil) can be used but is usually not as effective as chemical control, and it results in the loss of soil that has high moisture- and nutrient-holding capacity (Fleming *et al.* 1998). Early site preparation, with spring, autumn and post-planting herbicide application, is probably optimal to ensure adequate weed control, particularly on ex-agricultural pasture sites (Fleming *et al.* 1998; Nilsson and Orlander 1999).

Conclusions

This review has outlined the potential factors that cause transplant shock in tree seedlings in the context of plant acclimatisation and environmental conditions at planting. The area most widely studied has been the effect of site preparation. The areas most neglected by researchers, and those that may have the greatest economic impact on improved seedling survival and growth, are the physiology of seedling planting condition, particularly in relation to frost and drought tolerance. Thus there are opportunities to foster new research into the mitigation of transplant shock that can decrease the occurrence of seedling mortality and impaired growth at planting. Such research will also lead to general improvements in nursery practices that will include 'physiological hardening' as a tool for producing seedlings suited to a range of planting environments.

Acknowledgements

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