Industry Experiences and Research with Tissue Proliferation

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Tissue proliferation (TP) is characterized by a mass of woody tissue that typically forms on the main stem of plants near the soil surface. Frequently, but not always, small shoots may emerge from the TP. The size of the TP is normally proportional to the age of the plant and is seldom observed on plants until 2 to 3 years after propagation. The size of the TP ranges from 6 to 40 mm in diameter. TP is often loosely attached to the stem.

In 1992, TP was first described and reported to occur on certain cultivars of elepidote *Rhododendron* (American Nurseryman, 1992; Brand, 1992; LaMondia, 1992). Since that time, TP has been diagnosed and reported to occur in: Connecticut, Georgia, Massachusetts, Michigan, North Carolina, New York, Ohio, Oregon, Pennsylvania, Rhode Island, Virginia, Washington, and West Virginia in the United States, and Canada and the United Kingdom.

Tissue proliferation was first noticed by a few growers in the late 1980s. Initially, because of its visual similarities to crown gall disease, and the absence of definitive information about TP, these growers, plant inspectors, regulatory officials, and researchers were concerned (American Nurseryman, 1992; LaMondia, 1992; Linderman, 1993; Rostan, 1992). Three causal groups or agents that may trigger TP were suggested (Linderman, 1993): pathogens, cultural factors, and lignotuber formation.

PATHOGENS

Crown gall, a disease caused by the bacterium *Agrobacterium tumefaciens,* has been reported to occur on rhododendron (Moore, 1986). In 1989, Briggs Nursery supported and cooperated with Larry Moore, Oregon State Univ., to determine if the callus-like growth occurring on rhododendron was crown gall. No suspect strains of *A. tumefaciens* isolated from rhododendron were found to be pathogenic on rhododendron upon reinoculation, nor did TP tissue react with T-DNA probes used to identify pathogenic *A. tumifaciens* strains (Moore, unpublished).

Morphology of tissue proliferation further distinguishes it from crown gall. The vascular system in crown gall is malformed; the vascular system in the tissue proliferation is differentiated normally. Vegetative shoots often emerge from the tissue proliferation, but rarely from crown gall. The tissue proliferation is normally woody and hard compared to the spongy, dissociated crown gall tissue.

Other biotic agents have been suggested and eliminated as possible causal agents for TP. *Erwinia herbicola* pv. *gypsophilae* is a bacterium that promotes gall formation on *Gypsophila paniculata* Per. (Clark, 1989). Attempts to isolate *E. herbicola* at Oregon State Univ. from the TP of rhododendron were unsuccessful (Fischer, unpublished). In a preliminary analysis, using the DAPI (4′-6-diamine-2-phenyl indole) staining procedure, no phytoplasmas were in tissue from rhododendron with TP (Ash, unpublished).

The bacterium *Nocardia vaccinii* is known to form galls on blueberries (*Vaccinium* spp.: *V. australe* Small x *V. ashei* Reade) at or immediately beneath the soil surface (Demaree, 1952). Literature reviews have failed to reveal if *N. vaccinii* will attack rhododendron, another member of the Ericacae, and produce TP-like symptoms.

CULTURAL FACTORS

Cultural triggers may exist that stimulate TP formation (Linderman, 1993; Maynard, 1995). This possibility may explain why variation exists in reporting or detecting TP, especially when several growers purchase their liners from the same supplier.

In preliminary experiments at Briggs Nursery, a variety of pesticides were screened to detect if there was a positive correlation with the occurrence of TP on rhododendron. Herbicides tested included: pendimethalin (Pennant), oxyfluorfen and pendimethalin (Ornamental Herbicide II), oxadiazon/napropamide (Ronstar/Devrinol), oryzalin (Surflan) and trifluralin and isoxaben (Snapshot TG). Two fungicides screened were metalaxyl (Subdue) and fosetyl-Al (Aliette). A series of preliminary experiments proved to be inconclusive as to whether any of these pesticides has an effect on occurrence of TP with rhododendron. Further research is warranted.

CYTOKININ HABITUATION

The use of high concentrations of cytokinins and other plant growth regulators in vitro may lead to a higher frequency of growth abnormalities in the regenerated plant. Besides inhibiting root formation in vitro, cytokinins used in high concentrations have been shown to induce abnormally compact or dwarfed plants (Jones, 1979; Smith and Nightingale, 1979). With several plants, including *Rhododendron* 'PJM', cytokinins have been credited for the increased branching and desirable ornamental habit of the plant (Ettinger and Preece, 1985).

Research has suggested that tissue-cultured rhododendrons be grown with low cytokinin levels to insure vigorous shoots with a minimum of variation (Brand, 1992; Pogany and Lineberger, 1990). No studies that we could find have investigated the possible link of cytokinin concentration in vitro and the occurrence of tissue proliferation on mature plants.

LIGNOTUBERS

Structures similar to TP on rhododendron have been described as lignotubers or burls. Lignotubers have been reported to occur on stems of species rhododendron and other ericaceous genera, in their native

Received for publication 22 Aug. 1996. Accepted for publication 23 Dec. 1996. Use of trade names does not imply endorsement of the products named nor criticism of similar ones not named. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

Chemical names used: metolachlor (Pennant) 2-chloro-*N*-(2-ethyl-6-methylphenyl)-*N*-(2-methoxy-1-methylethyl)acetamide (Ciba Geigy, Greensboro, N.C.); oxyfluoren + pendimethalin (Ornamental Herbicide II) 2-chloro-1-(3-ethoxy-4-nitrophenoxy)-4-trifluoro-methylbenzene and *N*-(1-ethylpropyl)-3,4-dimethyl-2,6-dintrobenzenamine (Scotts Co., Marysville, Ohio); oxadiazon (Ronstar) 2-tert-butyl-4-(2,4-dichloro-5-isopropoxyphenyl)-1,3,4-oxadiazonolin-5-one (Rhone-Poulenc Ag. Co., Research Triangle Park, N.C.); napropamide (Devrinol) (RS)-*N*,*N*-diethyl-2-(1-napthyloxy)propionamide, (Zeneca Ag. Products, Wilmington, Del.); oryzalin (Surflan) 3,5-Dinitro-N_4,N_4-dipropylsulfanilamide (DowElanco, Indianapolis); trifluralin (Treflan) μ,μ,μ-Trifluoro-2,6-dinitro-*N*,*N*-dipropyl-p-toluidine, (DowElanco, Indianapolis); isoxaben + treflan (Snapshot TG) *N*-[3-(1-ethyl-1-methylpropyl)-5-isoxazolyl]-2,6-dimethoxybenzamide and μ,μ,μ-Trifluoro-2,6-dinitro-*N*,*N*-dipropyl-p-toluidine (DowElanco, Indianapolis); metalaxyl (Subdue) *N*-(2,6 Dimethylphenyl)-*N*-(methoxyacetyl)-DL-alanine methyl ester, (Ciba Geigy, Greensboro, N.C.); fosetyl-aluminum (Aliette) Aluminum tris (O-ethyl phosphonate), (Rhone-Poulenc Ag. Co., Research Triangle Park, N.C.); 2iP, N^6-[2-Isopentenyl]adenine (Sigma Chemical Co., St. Louis); acephate (Orthene) *O*,*S*-Dimethyl acetylphosphoramidothioate (Valent U.S.A. Corp., Walnut Creek, Calif.); bendiocarb (Turcam) 2,2-dimethyl-1,3-benzodioxol-4-yl methylcarbamate (AgrEvo U.S.A. Co., Wilmington, Del.); methiocarb (Grand Slam) 3,5-Dimethyl-4-(methylthio)phenyl methylcarbamate (Olympic Horticultural Products Co., Mainland, Pa.); triadimefon (Bayleton) 1-(4-Chlorophenoxy)-3,3-dimethyl-1-(1*H*-1,2,4-triazol-1-yl)-2-butanone (Bayer Corp., Agriculture Div., Kansas City, Mo.); propiconazole (Banner) 1-[2-(2,4-dichlorophenyl)-4-propyl-1,3-dioxolan-2-yl]methyl]-1*H*-1,2,4-triazole (Ciba Geigy, Research Triangle Park, N.C.).

habitat: *Arbutus* sp., *Arctostaphylos glandulosa* Eastw., *A. tomentosa* Lindl., *A. rudis* Jeps and Wiesl., *A. patula* Greene, *Erica arborea* L., *E. verticillata* Bergius, *Kalmia latifolia* L., *Rhododendron burmanicum* Hutch., *R. cilliicalyx* Franch., *R. macrophyllum* (*californicum*) D.Don, *R. maximum* L., *R. occidentale* A. Gray, *R. scottianum* Scott (Barrett, 1941; Del Tredici, 1992; Garland, 1960; James, 1984; Peattie, 1950; Sinclair, 1987; B. Smith, personal communication). James (1984) speculated that several other ericaceous taxa may also possess lignotubers or burls. Lignotubers are bud burls produced at or near the root collar—being partly or entirely subterranean. These structures are part of the normal ontogeny of certain plants. Lignotubers are often produced as an adaptation for regrowth after injury to the stem and are commonly found on plants that grow in stressful environments such as in Mediterranean climates where fire is an important part of the ecology, or in areas where drought, grazing, or browsing occur. The wood of the lignotuber is generally dense, heavy with a swirled grain, and fire resistant (Barrett, 1941; Garland, 1960). Lignotuber formation can be used as a taxonomic trait and is a heritable characteristic (Garland, 1960).

Many nurserymen still collect *Kalmia latifolia* from native stands in the Appalachian Mountains as burls or laurel plates. These plants are severely cut back and planted in nursery rows. The plants branch heavily from the basal lignotuber, are grown on, and then sold (Del Tredici, 1992).

Lignotubers may be a possible explanation for TP. There are differences and similarities with these structures. TP structures are formed more quickly and are not as dense as lignotubers, which are formed slowly with a dense, heavy wood. However, vessel and trachea length within the TP on *Rhododendron* cultivars Lee's Dark Purple and Solidarity were significantly shorter than in adjacent root and stem tissues of the same plants. This result is consistent with lignotuber data for *Arctostaphylos* (James, unpublished).

This paper will evaluate 1) if TP could be produced by the bacterium, *Nocardia vaccinni*, 2) if TP occurrence is affected by fertilizer applications, 3) if TP is associated with common ancestors, and 4) what affect modifying the cytokinin levels used in micropropagation may have on the occurrence of TP.

EXPERIMENTS CONDUCTED

Inoculation of rhododendron with Nocardia. The bacterium *Nocardia vaccinii* n. sp. was obtained from the American Type Culture Collection and suspended in sterile deionized water to a concentration of 1×10^6 colony-forming-units/mL. Ten replicate, 3-year-old, TP-absent, 'Nova Zembla' rhododendron plants growing in 3.8-L nursery containers filled with 100% Douglas fir bark media were inoculated. The bacterial suspension was injected into the phloem with a syringe near the soil line. The control was an injection of sterile deionized water. After inoculation, plants were grown 1 year under nursery conditions and evaluated for TP.

Effect of plant growth/fertilizer amount on the occurrence of TP. Rhododendron 'Solidarity' was grown for 19 months in 20-cm-diameter (7.6-L) nursery containers using two fertilizer regimes. Fifty plants were potted 1 Mar. 1994 in 100% Douglas fir bark medium and top-dressed with 12 g (low rate) of Grace Sierra/Controlled Release Fertilizer 21–4–7 High N + Mg and Fe (19.0% N; 1.3% P; 5.8% K; 1.5% Mg; 2.0% Fe) (Grace Sierra Horticultural Products Co., Milpitas, Calif.). An additional 50 plants of the same clone were also potted into 7.6-L containers, but were top-dressed with 24 g (high rate) of the same fertilizer. For plants requiring low fertility, Grace Sierra recommended a fertilizer application of 20 g/7.6-L container. Plants were watered as required, but no other form of nutrients was applied to these plants. On 9 Mar. 1995, the same fertilizer was reapplied at corresponding rates to each of the respective treatments. On 6 Oct. 1995, surviving plants were examined, growth index (height × number of branches) determined, and presence or absence of tissue proliferation recorded.

Association of TP with common ancestors. Rhododendron selections have been surveyed yearly since 1989 at Briggs Nursery for the prevalence and frequency of TP. All container-grown rhododendrons were visually and physically examined during September–November. Physical examination involved hand-probing down the main stem into the upper root ball. The genealogies were compiled for nine cultivars most prone to form TP by referring to plant registrations and reference material (Salley, 1992).

Effect of in vitro cytokinin (2iP) level on the occurrence of TP. The cytokinin 2iP was examined to determine its influence on the development of TP on rhododendron. Tissue-cultured rhododendrons were subcultured five times with experimental media containing four concentrations of the 2iP (0.04, 0.4, 2.0, 8.0 μM). Five rhododendron cultivars were tested: 'Chionoides', 'The Honorable Jean Marie de Montague', 'Nova Zembla', 'PJM', and 'Solidarity'. Shoots were rooted in vitro and established using typical production methods (Anderson, 1978). Plants were grown in 20-cm-diameter nursery containers filed with 100% Douglas fir bark medium and grown for 26 months. Plants received herbicide, napropamide (4.50 kg a.i./ha) 23 June 1993; and napropamide (4.50 kg a.i./ha) plus oxadiazon (2.25 kg a.i./ha) 19 Apr. 1994. Insecticides and fungicides were applied to the point of run-off. Insecticide applications were: acephate (0.9g a.i./L), 28 June 1993; bendiocarb (0.9g a.i./L), 17 July 1993; methiocarb (3.6g a.i./L), 14 Aug. 1993; bendiocarb (0.9g a.i./L), 8 June 1994; bendiocarb (0.9g a.i./L), 16 July 1994. Fungicide applications were triadimefon (0.2g a.i./L), 14 Aug. 1993, and propiconazole (0.067 ml a.i./L), 5 May 1994. Final data were collected for TP occurrence on 15 Aug. 1995. All plants were visually and physically evaluated for presence or absence of TP.

FINDINGS

No galling was apparent after inoculation with the bacterium *Nocardia vaccinnii* n. sp., or with the sterile deionized water control with the rhododendron 'Nova Zembla'. Although this bacterium has been reported to produce TP-like symptoms on blueberry seedlings, with bud-proliferating galls occurring at or immediately below the soil line (Demaree and Smith, 1952), no symptoms appeared on the 'Nova Zembla' plants. This is consistent with Demaree and Smith's (1952) finding that when azalea was inoculated with their strain of *Nocardia vaccinnii* n. sp., the azalea did not produce galls.

High fertilization rates increase tissue proliferation. The number of plants on which TP developed was significantly higher in the high fertilization treatment, where 29 of 47 plants developed TP over 19 months; only 11 of 47 plants in the low-fertilizer rate treatment developed TP. Interestingly, not only were plants larger in the high-fertilizer treatment, but TP occurrence was also significantly more common with the high-fertilizer treatment. In further analysis, plants were grouped within each fertilizer treatment into four size groups: the median number of plants, number of plants with TP, and plant size in each group. There was a high linear correlation ($r = 0.9399$) for TP number and median plant size for all treatments (Fig. 1). This result is consistent with suggestions that plant culture may have a significant effect on the occurrence or development of TP (Linderman, 1993; Maynard, 1995).

Genotype has a significant effect on tissue proliferation. A survey of rhododendron cultivars highly prone to form TP and a review of their genealogy identifies some common ancestors (Table 1). Of the cultivars listed, three were hybrids of 'The Honorable Jean Marie de Montague' and one was this particular cultivar. The species *R. yakushimanum* Nakai. and *R. griffithianum* Wight were the most common species in the background of the hybrids listed. As several species of rhododendron have been described as forming lignotubers or regenerative structures, it would be intriguing to investigate the species listed in Table 1 for the presence of these structures.

A range of cytokinin concentrations from 0.04 to 8.0 μM had no affect on tissue proliferation. The occurrence of TP was significantly related to genotype, with highest occurrences on 'Solidarity' and 'The Honorable Jean Marie de Montague' (Fig. 2). Therefore, assuming that a cultivar must be susceptible to TP before cytokinin concentration would have an affect, these two TP-prone cultivars were used in evaluating the effect of cytokinin concentration in the propagation medium on the occurrence of TP as observed 3 years later: cytokinin had no significant or consistent effect on the incidence of tissue proliferation of these two TP-susceptible cultivars.

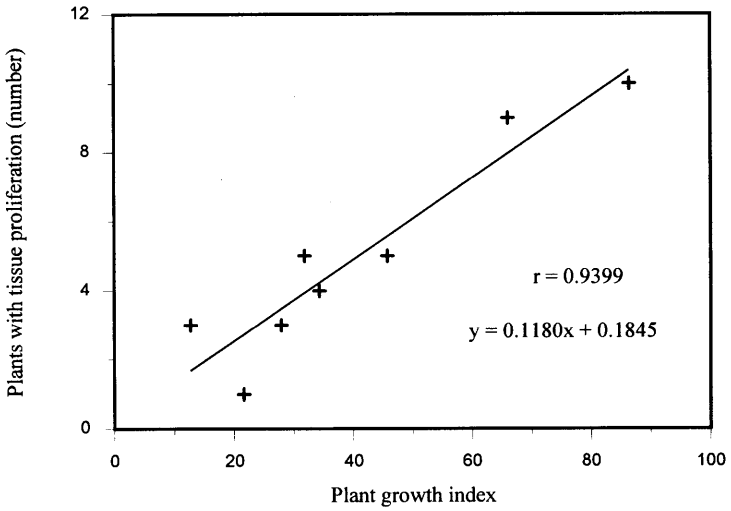

Fig. 1. The correlation between the number of plants with tissue proliferation and plant growth index (plant height × number of branches).

Table 1. Rhododendron cultivars with parentage and genealogy (Salley, 1992) that have consistently demonstrated a high incidence of tissue proliferation.

Cultivar	Genealogy
Aloha	Vulcan x *R. yakushimanum* 25% *R. griersonianum*, 12.5% *R. griffithianum*, 50% *R. yakushimanum*
Bambino	(Brittania x *R. yakushimanum*) x Lem's Cameo 3% *R. arboreum*, 12.5% *R. decorum*, 12.5% *R. dicroanthum*, 21% *R. griffithianum* 50% *R. yakushimanum*
Centennial Celebration	Purple Lace x *R. yakushimanum* 6% *R. griffithianum*, 12% *R. ponticum*, 50% *R. yakushimanum*
Dopey	[(*R. facetum* x ?) x Fabia] x (*R. yakushimanum* x Fabia Tangerine) 25% *R. dicroanthum*, 12.5% *R. facetum*, 25% *R. griersonianum*, 25% *R. yakushimanum*
Grace Seabrook	The Honorable Jean Marie de Montague x *R. strigillosum* 25% *R. griffithianum*, 50% *R. strigillosum*
Hallelujah	Kimberly x The Honorable Jean Marie de Montague 25% *R. fortunei*, 25% *R. griffithianum* 25% *R. williamsianum*,
Marlene Peste	(*R. yakushimanum* x Corona) x *R. haematodes* 50% *R. haematodes* 25% *R. yakushimanum*
Solidarity	The Honorable Jean Marie de Montague x *R. yakushimanum* 25% *R. griffithianum*, 50% *R. yakushimanum*
The Honorable Jean Marie de Montague	*R. griffithianum* x ? 50% *R. griffithianum*

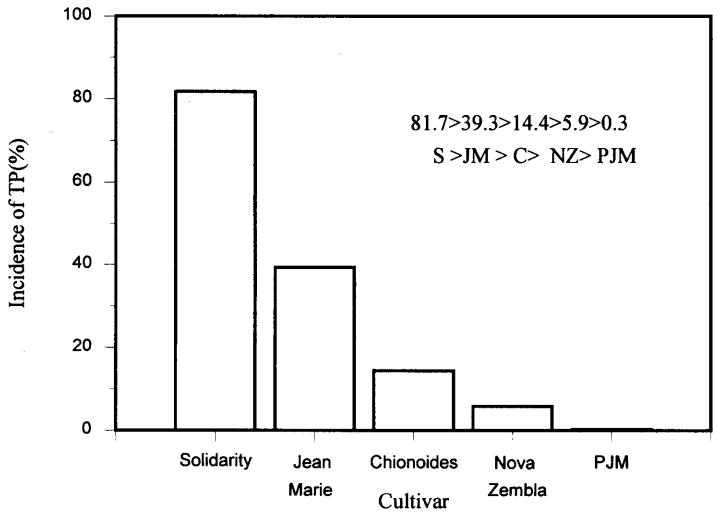

Fig. 2. Genotype is a significant determinant of tissue proliferation. Genotype effect on TP was significant at $P \leq 0.001$.

CONCLUSIONS AND RECOMMENDATIONS

We agree with the hypothesis that TP may be a structure similar to a lignotuber. But, because plants are grown in a nursery production environment with accelerated growth conditions, the lignotubers produced are abnormal and malformed in their morphology and unable to regrow. Additional research is needed to identify if other cultural factors may affect the occurrence of TP. Anatomical research will reflect any relationships between lignotuber and TP. Breeding studies should be conducted to examine the heritability of TP. These possibilities need to be further investigated to understand the nature of and possible triggers to the occurrence of TP.

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The Induction of Tissue Proliferation-like Characteristics in In Vitro Cultures of *Rhododendron* 'Montego'

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The term tissue proliferation (TP) was first employed by a workgroup of growers, research scientists and Oregon and Washington Dept. of Agriculture officials (Obermire and Milbrath, unpublished). TP is described as an abnormal callus-like growth produced at or near the crown of a plant (LaMondia et al., 1992). The tumors may or may not be accompanied by a proliferation of shoots and buds (Brand and Kiyomoto, 1992; Linderman, 1993). TP shoots are small, with short internodes and a whorled-leaf arrangement (Brand, 1992a). These shoots are short-lived, and die off regularly, only to be replaced by new shoots (Brand, 1992a).

TP has been reported in numerous locations in the continental United States and in Europe (LaMondia et al., 1992). Genera in which TP has been observed include *Rhododendron*, *Kalmia*, and *Pieris* (Linderman, 1993), but TP occurrence has been most problematic in *Rhododendron*. Various *Rhododendron* cultivars, mostly elepidotes, have been observed with TP symptoms (Brand and Kiyomoto, 1992; Linderman, 1993).

Received for publication 22 Aug. 1996. Accepted for publication 23 Dec. 1996. Storrs Agricultural Experiment Station scientific contribution no. 1656. This research was funded in part by funds made available through the Holden Arboretum, Mentor, Ohio. The cost of publishing this paper was defrayed in part by the payment of page charges. Under postal regulations, this paper therefore must be hereby marked *advertisement* solely to indicate this fact.

The occurrence of TP on *Rhododendron* was not reported until the widespread use of plants originating from tissue culture (Brand, 1992a). Although some growers report occasionally observing TP on seedling and cutting-propagated plants, the vast majority of plants developing TP have been micropropagated. The symptoms of TP become most noticeable on plants 2 to 5 years following propagation (LaMondia et al., 1992). Close inspection of young micropropagated plants reveals that TP tumors and symptoms are evident well before reaching mature nursery size. The effect TP has on plant health is unknown, and landscape performance of rhododendrons with TP has been questioned. Experimental evidence is required to determine the biological basis of TP to remedy its occurrence (Brand and Kiyomoto, 1992).

Because of the similarities between TP symptoms and crown gall, *Agrobacterium* involvement has been suspected as a possible cause for TP. Investigations searching for supportive evidence of *Agrobacterium*'s role in TP have strongly indicated that TP is not caused by *Agrobacterium tumefaciens* (Linderman, 1993). Evidence for the involvement of other microbial agents or mycoplasma-like organisms in TP has not been found (Linderman, 1993). Additional evidence against a pathogenic cause for TP is supported by the observation that TP in rhododendrons does not appear to be highly contagious (American Nurseryman, 1992). Although TP does not appear to be pathogen-induced, this possibility still remains viable.