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Tree Physiology review

Epicormic buds in trees: a review of bud establishment, development and dormancy release

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The formation of epicormic sprouts on the boles of trees is a phenomenon that has, until recently, been poorly understood. Renewed interest in the topic in the last two decades has led to significant advances in our knowledge of the subject, especially in regard to bud anatomy, morphology and ontogeny. There exists, however, no comprehensive synthesis of results from different disciplines across genera and geographical areas; this review seeks to fill that void and provide a comprehensive framework capable of guiding future research. A tree's potential for producing epicormic branches is dependent on the number of buds that are produced on a growing shoot, the development of those buds and associated meristems over time and the factors that promote sprout formation or bud death. Based on the descriptions of a limited number of researched species, we were able to describe four different developmental strategies for epicormics based on characteristics of meristem development. Control over epicormic bud dormancy is complex, but it is clear that the traditional view of auxin-mediated dormancy release is incomplete. Genetic control over epicormic development is yet to be empirically proven. Future research should focus on clarifying these physiological and genetic controls of epicormic bud development as well as developing more robust methods for tracking epicormics in ecological and silvicultural studies.

Keywords: bud development, epicormic branches, epicormic potential, silviculture, water sprouts, woody plants.

Introduction

Epicormic branches are branches that sprout from dormant buds on shoots that elongated in a previous period of growth. These branches are an issue of particular concern to forest managers when they form on the boles of potentially high-value trees (Harmer 1991) because they can greatly influence tree quality and reduce stem value (Büsgen and Münch 1929, Kerr and Harmer 2001). Epicormic branch formation has been generally thought to be a response to light (Bernsten 1961, Blum 1963, Smith 1965) or stress (Stone and Stone 1943, Burrows 2008), moderated by genetic variation, both among trees within a species (Ward 1966, Bowersox and Ward 1968) and among species (Büsgen and Münch 1929, Rey-Lescure 1982, Meadows 1995, Burrows 2002, Burrows et al. 2010).

Recent research has provided many new insights into the anatomy and ontogeny of epicormic buds and branches (e.g., Fontaine et al. 1998, 1999, 2001, Burrows 2000, 2002, Colin et al. 2010a, 2010b, Morisset et al. 2012a, 2012b), but significant gaps in our knowledge remain. For example, a greater understanding is still needed of the physiological, ontogenetic and environmental factors that underlie epicormic bud development and sprouting in a wider variety of species.

The topic of annual bud dormancy in woody plants has been widely reviewed (e.g., Saure 1985, Champagnat 1989, Rohde et al. 2000, Arora et al. 2003). However, apart from two reviews of the physiology and ecology of epicormic sprout development and persistence in conifers (Ishii et al. 2007, Ishii 2011), there is no comprehensive review on the developmental dynamics of epicormic buds in trees. There are also few integrated theories

Table 1. Various terminology in the literature for epicormic structures in different contexts.

Epicormic structure	Context	Term	Citation
Branch	Forest management	Bole sprout	Erdmann and Peterson (1972)
	Forest management	Secondary shoot	Spiecker (1991), Springmann et al. (2011)
	Forest management	Water sprout	Büsgen and Münch (1929), Spiecker (1991)
	Ontogeny	Preventitious shoot	Gruber (1994)
	Tree architecture	Delayed branch	Barthélémy and Caraglio (2007)
Bud	Ontogeny	Preventitious	Gruber (1994), Wilson and Kelty (1994),
		(proventitious) bud	Fontaine et al. (1998, 1999)
	Physiology	Dormant bud	Büsgen and Münch (1929), Stone and Stone (1943), Church and Godman (1966), Spiecker (1991), Bégin and Filion (1999)
		Latent bud	Schweingruber et al. (2006), Lauri et al. (2008)
	Physiology	Suppressed bud	Kormanik and Brown (1969), Brown (1971), Bryan and Lanner (1981)
	Tree architecture	Reserve bud	Tomlinson (1983), Wilson and Kelty (1994)
	Trace	Anatomy	Medullary ray
Anatomy		Stele	Church and Godman (1966)
Anatomy		Vascular trace	Brown (1971), Fontaine et al. (1999)
Physiology		Dormant bud strand	Bernsten (1961)

of epicormic branch formation (Ishii et al. 2007). Those that have been published implicate inter- and intra-specific genetic variation, perturbations in the surrounding environment and tree-level stress as three of the most important factors influencing epicormic development (Meadows 1995, Colin et al. 2010a). The inclusion of epicormic ontogeny is also critical (Colin et al. 2010a), especially in terms of bud initiation, development and dormancy release (Fontaine et al. 2001, Colin et al. 2010c).

A main objective of this review is to synthesize recent research with historical studies, drawing inferences from the extensive literature describing similar physiological processes in other tree buds when needed to support our descriptions and conclusions. We will emphasize the morphological and physiological underpinnings of epicormic bud formation and sprouting in trees, with a focus on bud dynamics prior to epicormic branch formation. We will begin with a discussion on the terminology associated with epicormic structures, followed by a comparison of epicormic buds described in the literature and factors influencing their establishment and development. The release of dormancy in epicormic buds will then be reviewed, with a focus on physiological processes and the impact of environment and ontogeny on those processes. Next, we will address the applicability of interesting new insights from molecular studies of axillary bud dormancy in herbaceous plants, and consider how genetics may influence epicormic tendencies. Finally, we will conclude by describing a generalized theory of epicormic bud control from bud establishment to sprouting and propose future research directions.

Terminology

There is a need for standardization of the terminology associated with epicormics as terms associated with the same

anatomical structures vary widely based on scientific discipline and context (Table 1). Fundamentally however, an epicormic branch must develop from a dormant bud on a non-succulent shoot (Waters et al. 2010). These dormant buds expand subsequent to the regular development of sequential branches (Figure 1g) that elongate with the initial flush of a growth unit (Bryan and Lanner 1981, Gruber 1994).

Therefore, we propose that all vegetative buds and meristems on old growth units be called epicormic buds or meristems (sensu Burrows 2000, Del Tredici 2001, Gordon et al. 2006, Colin et al. 2010a). Groups of epicormics originating from an original epicormic bud should be referred to generally as epicormic complexes (Table 2). Individual units within a larger feature, such as organs within a bud or buds and branches within an epicormic complex, should be considered epicormic components. All the individual components associated with a given feature will be referred to jointly as the epicormic structure. The combination of all epicormic complexes on a tree will be called the epicormic composition (Colin et al. 2010b). Changes over time in the characteristics of epicormic buds, complexes or composition will be called epicormic development.

For the purposes of this review, any buds that are established concurrently with the shoot elongation will be called sequential buds (Figure 1c); branches sprouting from these buds will be considered sequential branches (Hallé et al. 1978, Nicolini et al. 2003) (Figure 1g). Some buds on old growth units are cauliferous, that is, they produce reproductive structures (Fink 1999). Fink (1983) differentiates epicormic and cauliferous buds based on whether they are vegetative or reproductive. Therefore, if the bud has differentiated generative organs, it should not be considered epicormic. We assume, in lieu of evidence to the contrary, that all other live buds on an

old growth unit are vegetative and, given the proper stimulus, are able to produce epicormic sprouts. Buds that produce stump sprouts share generally the same ontogeny as other

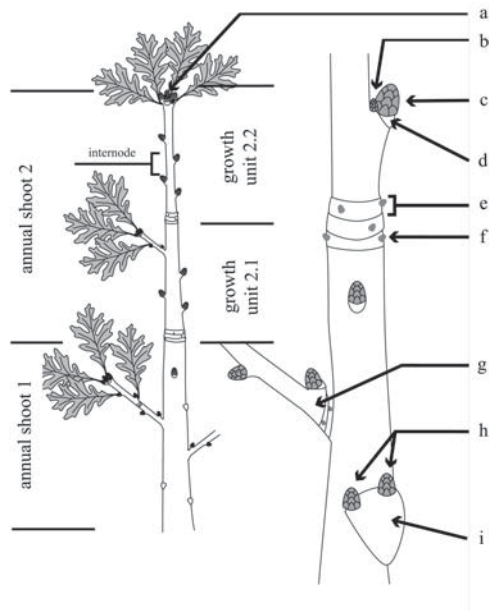


Figure 1. Generalized shoot of an oak with different bud types and growth terms identified. All buds are sequential buds with the exception of a and g. Letters identify the following: a, terminal bud; b, collateral accessory bud; c, sequential bud; d, leaf scar; e, cataphyll or bud scale scar; f, cataphyll or bud scale bud; g, sequential branch; h, secondary accessory buds; i, bud scar formed following the death of a sequential bud. Drawn based on Heuret et al. (2003).

epicormic buds and will be considered as epicormic for the purpose of this review. Buds that produce root sprouts are in some sense anatomically similar to above-ground preventitious and adventitious buds (Bosela and Ewers 1997, Del Tredici 2001); however, developmental and physiological differences between above- and below-ground structures prohibit direct comparison.

Anatomy and morphology of epicormic structures

Epicormic buds can be differentiated into adventitious and preventitious (or proventitious, cf. Gruber 1994, Fontaine et al. 1998, Colin et al. 2010a) types (Büsgen and Münch 1929, Fink 1983, Spiecker 1991). The key difference between the two types is developmental; preventitious buds originate exogenously and descend from a shoot apical meristem, while adventitious buds develop endogenously from previously non-meristematic tissue (Brown 1971, Fink 1999).

Preventitious structures

In most cases, the presence of a continuous series of cells associated with the development of vascular tissue, which we will refer to as an epicormic trace (for alternative nomenclature, see Table 1), is sufficient to distinguish preventitious from adventitious epicormic structures (Figure 2) (Büsgen and Münch 1929, Spiecker 1991). This non-functional trace is composed mainly of parenchyma cells (Cremer 1972, Fontaine et al. 1999, Waters et al. 2010) and leads from the epicormic structure to the pith of its parent shoot (Bryan and Lanner

Table 2. Definitions of some terms used often throughout this paper.

Term	Definition	Citation
Epicormic complex	Groups of epicormic buds and/or branches resulting from the development of an original epicormic bud.	Fink (1999)
Epicormic component	Individual units within a larger epicormic feature. Cells, meristems and leaf primordia are all components of an epicormic bud; epicormic buds, branches and traces may be components of an epicormic complex.	
Epicormic composition	The composition of all epicormic complexes on a given tree.	Colin et al. (2010b)
Epicormic development	Progressive increase in size and complexity of individual structures within an epicormic bud or epicormic complex.	Colin et al. (2010b)
Epicormic ontogeny	'The course of development of epicormics, including their possible transformations from one class to another.'	Colin et al. (2010b)
Epicormic strand	Meristem descended from an initial axillary bud and subsequently buried in the bark. No bud-like organization is regularly present, and the strand expands over time.	Burrows (2002)
Epicormic structure	All of the individual components of a given epicormic feature. The vascular trace, leaf and bud scale primordia, and shoot apical meristem are collectively an epicormic structure.	
High bud	Distinct epicormic bud on the bark surface with a meristem enclosed in bud scales.	Fink (1980a)
Flat bud	Small epicormic bud that rises only slightly above the bark surface. Bud scales are incorporated into the bark.	Fink (1980a)
Deep bud	Bud buried in a cavity within the bark, with bud scales lining the cavity. Leaf primordia may be present with the meristem.	Fink (1980a)
Shoot-germ	Meristematic bud base buried in the bark following loss of the bud tip. Only residual meristematic tissue is present.	Fink (1980a)

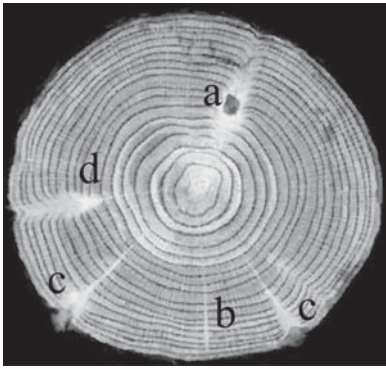


Figure 2. Interior structure of an oak log showing epicormic structures. Structures are identified as: a, knot of a sequential or regular branch; b, primary living epicormic bud with only minor trace expansion signifying that it has not sprouted; c, sprouted epicormic buds showing distinct bud traces and expansion of the bud trace at the time of sprouting as well as development across the cambium; d, primary epicormic sprout that sprouted 7 years after initiation and subsequently died.

1981, Kauppi et al. 1987, Fontaine et al. 1999), providing evidence of the continuous presence of a viable apical meristem. Regardless of whether an epicormic meristem forms on the central shoot or on a sequential branch, the trace almost always is oriented at an angle nearly perpendicular to the pith of the main tree stem (Büsgen and Münch 1929, Cremer 1972, Bryan and Lanner 1981, Colin et al. 2010c). In many cases, buds initially form on a sequential branch (Figure 1g), but branch shedding and bud migration can cause the buds to appear externally as if the structure developed on the bole itself (Blum 1963, Cremer 1972, Bryan and Lanner 1981). Radial extension of the trace at the rate of overall diameter growth of the tree enables the meristem to be maintained in its position on or in the bark (Church and Godman 1966, Fink 1980a, Kauppi et al. 1987).

The epicormic meristem often develops within a bud on the bark surface. It is enclosed in bud scales and maintains a vascular connection with the tree. Leaf primordia may be present (Fink 1980a, 1983), but more often are not (Fink 1980a, Gruber 1994, Fontaine et al. 1998, 1999). Preventitious meristems also occur within the bark either as buried buds, shoot germs (Fink 1980a, 1983) or as epicormic strands that do not exhibit bud-like organization (Cremer 1972, Burrows 2000). In some cases, preventitious epicormic structures may consist only of meristematic cells in the leaf axils (Fink 1984, Burrows 1990, Burrows et al. 2003). Epicormic traces are established only after a period of time in these meristems only if and when they are stimulated to produce a bud. Therefore, an epicormic trace is not an essential feature of a preventitious epicormic structure (Fink 1999).

Adventitious structures

Adventitious buds generally originate independently from annual shoot growth, though in a few species they constitute an important component of plant development (Fink 1983, 1999).

They are not initially connected to the pith of a shoot but instead develop in situ, most often in callus tissue at wounding sites (Fink 1983, 1999, Kauppi et al. 1987). Subsequent development of vascular tissues initiates an epicormic trace; thereafter, a continuous epicormic trace is present in the wood (Kormanik and Brown 1969, Burrows 1990). Many early studies describing adventitious shoot formation may have been incorrect since assessments were made based on macroscopic investigations. On close inspection epicormic bud development can often be followed back to a parent bud (Stone and Stone 1943, Brown 1971, Burrows 2002). Although some authors limit their use of the term epicormic to preventitious structures (e.g., Bryan and Lanner 1981), most of the relevant literature includes adventitious buds and branches as epicormics (Büsgen and Münch 1929, Brown 1971, Fink 1983, Fontaine et al. 1998).

Development of epicormic structures

Epicormic bud initiation

The first and most critical factor influencing epicormic bud initiation in trees is the 'genetic growth plan' (Hallé et al. 1978) of an individual species, which may be strongly moderated by the environment (Tomlinson 1983, Bellingham and Sparrow 2000, Vesik 2006). In the context of epicormics, this initially means that the most significant variation among individual species is their genetically determined developmental pathway, since the number, type and location of sequential buds on an annual shoot are important determinants of future epicormic branch development (Morisset et al. 2012b).

The number of buds on an annual shoot has an impact on the number of epicormic buds that form, but the persistence of the initial buds is even more important. Large sequential buds (Figure 1c) do not, in most cases, become epicormic buds (Cremer 1972, Wilson 1979, Harmer 1991, Wilson and Kelty 1994, Remphrey et al. 2002), though epicormic buds often originate in their axils (Figure 1b and h) (Church and Godman 1966, Kormanik and Brown 1969, Fink 1980a, Braham and Kellison 1987, Kauppi et al. 1987, Burrows 2000). When a terminal (Figure 1a) or sequential bud sprouts, multiple small axillary buds occur in the bud scale scars at the base of the resultant shoot (Figure 1e and f). These are more likely than large buds to persist as epicormics, meaning that the sprouting of a sequential bud has the potential to increase the total number of epicormic buds (Cremer 1972, Bryan and Lanner 1981, Fontaine et al. 1998, 2001, Colin et al. 2010a).

The rate of annual height growth is another factor that influences the number of epicormic buds. For *Quercus petraea* (Matt.) Liebl., which has the potential to produce multiple growth units in a single growing season, the total number of buds produced is related both to the total number of growth

units and to the length and number of internodes within each growth unit (Harmer 1989, Collet et al. 1997). Although the total number of buds is well correlated with the length of a growth unit, trees with multiple growth units in an annual shoot generally exhibit greater average internode lengths (Collet et al. 1997) and therefore fewer sequential buds per meter (Harmer 1989). However, the production of multiple growth units in a given year also stimulates sprouting of buds on earlier growth units (Harmer 1989), thus potentially increasing the overall number of buds. In some other species, axillary bud production is apparently higher when vigor is low (Gill and Tomlinson 1971, Braham and Kellison 1987). Broad comparisons among species, however, may not be entirely valid, because of interspecific variation and differences in the developmental processes involved in each case. Contrasting the total number of buds formed per unit area on a synonymous growth unit among different species with uniform treatments could more clearly elucidate the impacts of plant nutrition on bud formation.

Bud development and the epicormic potential

In trees, the bud bank is considered to be the total number of buds, both sequential and epicormic, that are capable of sprouting at a given time (Wilson and Kelty 1994). The bank of epicormic buds alone has further been called the 'epicormic potential' (Fontaine et al. 2001, Colin et al. 2010b) and its composition is dependent on the longevity of individual epicormic buds or bud-producing meristems as well as the developmental dynamics of epicormic complexes. Both bud longevity and bud dynamics vary greatly among species.

The development of preventitious buds should follow a predictable trajectory (Blum 1963, Fontaine et al. 2001), and since adventitious buds in unwounded trees are yet to be shown as an important constituent of the bud bank in most species, the concept of epicormic potential is quite valuable in anticipating epicormic branch formation. Epicormic potential has been quantified only in young *Q. petraea* trees (Fontaine et al. 2001), which showed a general decrease in the number of buds after a period of 2 years. Although multiple new buds were produced at the base of each bud that sprouted into an epicormic branch (thereby increasing epicormic potential), the number of buds that died without sprouting was high enough to more than offset the newly formed buds. Individuals that are less susceptible to the proliferation of epicormic structures may exhaust their epicormic potential at a young age, thus effectively eliminating the possibility of epicormic shoot formation (Morisset et al. 2012b). Species that retain persistent meristems may increase in epicormic potential as they age (Fontaine et al. 1998, 1999, Burrows 2000), as long as physiological or ontogenetic again causes the buds to lose their sprouting ability.

Epicormic potential varies widely with species. Initially, species with more axillary buds should intuitively be more

susceptible to epicormic sprouting than those with fewer (Braham and Kellison 1987), though axillary bud development, sprouting or death are more important factors in determining epicormic branching potential (Harmer 1989, Morisset et al. 2012b). Species or individuals within a species that tend to produce developed epicormic structures may increase their epicormic potential over time (Little and Somes 1956, Braham and Kellison 1987, Spiecker 1991, Burrows 2000). For example, counts of the number of epicormic buds per meter for *Q. petraea* range from 50 to 70 (Fontaine et al. 2001, Colin et al. 2010c). In contrast, an unverified estimate of the number of epicormic strands in *Eucalyptus* spp. places the total epicormic potential at more than 300 meristems per meter (McArthur 1968).

Development of epicormic traces

Although the epicormic potential at a given time is informative, the fluctuations in epicormic potential over a tree's life probably provide greater insight into epicormic bud dynamics. However, anatomical studies only provide a snapshot and must infer developmental dynamics from differences in the components of young and old epicormic structures. Repeated sampling of individual meristems over time is not possible, but characteristics of epicormic traces in the wood reflect previous bud activity and can be used to make broader long-term inferences. Single, continuous traces indicate a single bud that has neither sprouted nor died (Figure 2b), while a trace that ends within the wood indicates the death of a bud (Figure 2d) (Cremer 1972, Fink 1980a). Single traces that show sudden and significant widening are evidence of sprout formation (Figure 2c) (Spiecker 1991). Over time, many traces become branched (Bryan and Lanner 1981, Braham and Kellison 1987, Fontaine et al. 1999, 2004), indicating increased epicormic complexity as trees age. Recent three-dimensional reconstructions of traces in *Q. petraea* logs are beginning to enable analysis of epicormic bud dynamics throughout the life of a tree (Colin et al. 2010c, Morisset et al. 2012a, 2012b) by allowing for the quantification of bud development and comparison of whole-tree-level bud dynamics between individual trees. The development of bud growth models could be an important next step.

Epicormic strategy

While the general trends of epicormic development described above are widely applicable, there is considerable variation among species in the anatomy and morphology of the epicormic meristem and associated tissues (Burrows et al. 2008). An array of distinct epicormic bud and meristem types have been described (Fink 1980a, 1984, Burrows 1990, 2000, Burrows et al. 2003); we propose that the prevailing epicormic composition on any given tree is representative of all trees within that species and that individual species can be

classified based on this composition. We will refer to this as a species' 'epicormic strategy.' We have identified four common epicormic strategies in part by expanding on some groupings described by Burrows et al. (2010) and based on the bud types of Fink (1980a; see Table 2). A number of species do not fit well into any of the four main categories, such as *Lophostemon* spp. (Burrows 2002, Burrows et al. 2010) and *Melaleuca* spp. (Burrows et al. 2010), suggesting that, as more anatomical descriptions of widespread genera become available, many more groupings will need to be added. A summary of studies that have provided sufficient details to differentiate species by epicormic strategy is given in Table 3.

The first of these strategies is the external clustering (EC) strategy in which trees produce relatively small, persistent axillary buds, which develop into epicormic complexes consisting of numerous buds and shoots (Colin et al. 2010b). Both high buds and flat buds (Fink 1980a) are common, and individual epicormic buds may be maintained for at least 40 years (Fink 1980a, Fontaine et al. 1999). This group is most pronounced in some genera of temperate angiosperms, with *Quercus* spp. being a well-studied example, but occurs to some degree in conifers as well. Bud life-spans in the conifers are generally shorter (e.g., Bryan and Lanner 1981, Gruber 1994, Ishii and Ford 2001). The second strategy, the isolated bud strategy (IB), is characterized by the initial production of larger external epicormic buds, mainly high buds, which are less persistent and less likely to form large clusters. Both gymnosperms and angiosperms occur in this group. In some of these species (e.g., *Salix alba* L. and *Picea abies* (L.) Karst, Fink 1980a), initial meristems are buried in the bark and persist for decades. Initial external buds in this group have a short lifespan, rarely >15 years (Gruber 1994), but buried meristems may persist for 50 years or more (Fink 1980a). The third strategy, called the detached meristem (DM) strategy (Fink 1984), has only been described in conifers (Fink 1984, Burrows 1990, Burrows et al. 2003). The DM strategy entails the maintenance of minimally developed meristems hidden in leaf axils. Despite being preventitious in origin, these meristems generally do not differentiate into other tissues without some stimulus. The fourth group, the epicormic strand (ES) strategy, is common in many Australian Myrtaceae and is characterized by the presence of extensive meristematic strands within the bark that are capable of producing a continuous series of ephemeral epicormic buds (Burrows 2000, 2002).

There is no distinct epicormic structure that clearly separates the EC and IB strategies, though the presence of extensive clustering is important in EC and the lack of it is indicative for the IB. A comparison between *Q. petraea* (Fontaine et al. 1999), a species in the first group, and *Salix* spp. (Fink 1980a, Sennerby-Forsse and Zsuffa 1995), a genus in the second group, shows these differences distinctly. Species within both groups maintain epicormic buds that are present on the bole

surface and in which differentiated organs are evident (Kauppi et al. 1987, Fontaine et al. 1998, 1999). These buds can be distinguished visually from sequential buds by their generally smaller size and often flat, triangular shape (Church and Godman 1966, Kauppi et al. 1987, Harmer 1991, Wilson and Kely 1994). In many cases, the one-year-old small axillary buds contain no leaf primordia, only bud scales and a terminal meristem (Kauppi et al. 1987, Gruber 1994, Fontaine et al. 1998, 1999).

In the EC strategy, internal development of epicormic buds proceeds annually and often includes the establishment of bud scales and meristems of secondary buds (Sennerby-Forsse and Zsuffa 1995, Fontaine et al. 1998, 1999). This bud development probably occurs as a result of partial dormancy release early in each growth period (Braham and Kellison 1987, Kauppi et al. 1987, Fink 1999); short shoots in some species are a result of greater dormancy release allowing slightly more development of the epicormic bud (Kormanik and Brown 1969, Kauppi et al. 1987, Fink 1999). In the long term, these buds may develop into diverse epicormic complexes (Fink 1999, Colin et al. 2010b). Although apical growth is minimal during partial dormancy release, it is a critical feature of the EC strategy that allows for buds to remain on the bark surface (Church and Godman 1966, Fink 1980a, Kauppi et al. 1987).

The IB strategy, in contrast, does not require bud persistence on the surface of the bole. In angiosperms, entire bud structures are engulfed in the bark and maintain bud-like organization, with the meristem enclosed in bud scales (Fink 1980a, 1983). Initial buds of the gymnosperms in this group are partially truncated in the process of bark formation, leaving only a meristematic bud base in the bark (Fink 1980a, 1983). Containing only a meristem, these structures should not be called buds but have been labeled as 'shoot-germs' (Fink 1980a). These buried buds probably account for the long-term epicormic potential in IB species.

The DM strategy is characterized by the prevalence of detached axillary meristems (Fink 1984). These meristems are present just below the bark surface and are not connected to the main vascular system of the tree (Fink 1984, Burrows 1990, Burrows et al. 2003). In most species, if not stimulated to differentiate bud tissues, these meristems are sloughed off with the bark in a few years (Fink 1984). In the Araucariaceae, detached meristems undergo annual development and may persist for many years, though bud and sprout formation occurs only with substantial stimulus (Burrows 1990). *Taxus baccata* L. (Taxaceae) and *Wollemia nobilis* W.G. Jones, K.D. Hill & J.M. Allen (Araucariaceae) are unique in this group in that cellular differentiation into buds occurs from these meristems without obvious external stimulus (Fink 1984, Burrows et al. 2003).

The ES strategy is based on recent studies of the epicormic complexes in species within the Myrtaceae (e.g., Burrows

Table 3. List of available anatomical and morphological studies of epicormic structures, with a brief description on reported morphological attributes. Blank spaces in columns indicate that a particular feature was either not described or not described completely enough to provide a concise delineation of a feature. Cells with more than one feature listed indicate that at some point in development, all of the features are present, or they are present in more than one area. Question marks indicate that the exact feature is not explicitly stated in the original study, but is assumed from evidence presented.

Family	Genus	Species	Meristem morphology ¹	Reported epicormic components ²	Location of epicormic structure ³	Location of bud trace initiation ⁴	Epicormic strategy ⁵	Citation
Araucariaceae	<i>Araucaria</i>	<i>angustifolia</i>	P	M	Co	Ax	DM	Fink (1983)
Araucariaceae	<i>Araucaria</i>	<i>cunninghamii</i>	P	M	C	Ax	DM	Burrows (1990)
Araucariaceae	<i>Wollemia</i>	<i>nobilis</i>	P	M, Bp, Lp, V	Ob	Ax	DM	Burrows et al. (2003)
Cupressaceae	<i>Cryptomeria</i>	<i>japonica</i>	P	DM		Ax	DM	Fink (1984)
Cupressaceae	<i>Sequoia</i>	<i>sempervirens</i>	P	DM		Ax	DM	Fink (1984)
Cupressaceae	<i>Sequoiadendron</i>	<i>gigantenum</i>	P	M		Ax	DM	Fink (1984)
Cupressaceae	<i>Thuja</i>	<i>occidentalis</i>	P	DM		Ax	DM	Fink (1984)
Cupressaceae	<i>Thujaopsis</i>	<i>dolabrata</i>	P	DM		Ax	DM	Fink (1984)
Pinaceae	<i>Abies</i>	<i>alba</i>	P	B, Bs, Lp, V	Co	Ax	IB	Fink (1980a, 1983), Gruber (1994)
Pinaceae	<i>Abies</i>	<i>balsamea</i>	P			Ax		Stone (1953)
Pinaceae	<i>Abies</i>	<i>concolor</i>	P			Ax		Stone (1953)
Pinaceae	<i>Larix</i>	<i>decidua</i>	P	M	Ob-lb		IB	Fink (1980a)
Pinaceae	<i>Larix</i>	<i>kaempferi</i>	P	M	Ob-lb		IB	Fink (1980a)
Pinaceae	<i>Picea</i>	<i>abies</i>	P	M	B-Ob	Ax	EC	Fink (1980a), Gruber (1994)
Pinaceae	<i>Picea</i>	<i>sitchensis</i>	P				IB	Herman (1964)
Pinaceae	<i>Picea</i>	<i>palustris</i>	P			Ax, La?	IB	Stone and Stone (1943)
Pinaceae	<i>Pinus</i>	<i>rigida</i>	P			La?	IB	Stone and Stone (1943)
Pinaceae	<i>Pseudotsuga</i>	<i>menziesii</i>	P	M, Bs, Lp	B		EC	Bryan and Lanner (1981)
Taxaceae	<i>Taxus</i>	<i>baccata</i>	P	B, Bs, V	B	Ax	DM	Fink (1980a, 1984)
Aceraceae	<i>Acer</i>	<i>pensylvanicum</i>	P	B, Lp	C	Bs	IB	Wilson (1979)
Aceraceae	<i>Acer</i>	<i>pseudoplatanus</i>	A, P	B, Lp, V	Co, B	Ax, Ad	EC	Fink (1983)
Aceraceae	<i>Acer</i>	<i>saccharum</i>	P			Ax*, Bs	IB	Blum (1963), Church and Godman (1966)
Betulaceae	<i>Alnus</i>	<i>rubra</i>	P			Ax*	EC	Bernsten (1961)
Betulaceae	<i>Betula</i>	<i>alleganiensis</i>	P			Ax*	EC	Blum (1963)
Betulaceae	<i>Betula</i>	<i>pubescens</i>	P	B, Bp, Lp, V	B	Ax	EC	Kauppi et al. (1987)
Clusiaceae	<i>Clusia</i>	<i>rosea</i>	A	M	Ph	L	DM?	Fink (1983)
Combretaceae	<i>Terminalia</i>	<i>arjuna</i>	P			Ax		Fink (1983)
Fagaceae	<i>Fagus</i>	<i>sylvatica</i>	A, P	B, Bs, V	B	Ax	IB?	Fink (1980a, 1980b)
Fagaceae	<i>Quercus</i>	<i>mongolica</i>	P			La	EC	Yokoi and Yamaguchi (1996)
Fagaceae	<i>Quercus</i>	<i>petraea</i>	P	B, Bp, C, Lp, V	B	Ax, Bs	EC	Fontaine et al. (1998, 1999)
Fagaceae	<i>Quercus</i>	<i>robur</i>	P	B, Bs, V	B	Ax	EC	Fink (1980a)
Fagaceae	<i>Quercus</i>	<i>rubra</i>	P	B, Bp, Bs, V	B	Ax	EC	Fink (1980a)
Hamamelidaceae	<i>Liquidambar</i>	<i>styraciflua</i>	P	Bp, Lp, V	B	Ax, Bs, Co	EC	Kormanik and Brown (1969)
Magnoliaceae	<i>Liriodendron</i>	<i>tulipifera</i>	P			Ax	EC	Braham and Kellison (1987)
Moraceae	<i>Ficus</i>	<i>religiosa</i>	A*, P	V	B, Ob		EC	Aloni and Wolf (1984)
Myrtaceae	<i>Allosyncarpia</i>	<i>ternata</i>	P	ES, B, Bp, C	Ob		ES?	Burrows et al. (2010)
Myrtaceae	<i>Angophora</i>	<i>hispidula</i>	P	ES, Bp, C	Ob-lb	Ax	ES	Burrows (2002)
Myrtaceae	<i>Angophora</i>	<i>melanoxylon</i>	P	ES, C		Ax	ES	Burrows (2002)

Continued

Table 3. Continued

Family	Genus	Species	Meristem morphology ¹	Reported epicormic components ²	Location of epicormic structure ³	Location of bud trace initiation ⁴	Epicormic strategy ⁵	Citation
Myrtaceae	<i>Corymbia</i>	spp.		ES, Bp	B-X		ES	Burrows et al. (2010)
Myrtaceae	<i>Eucalyptus</i>	<i>blakelyi</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>caesia</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>calophylla</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>cinerea</i>	P	ES, Bp, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>citriodora</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>cladocalyx</i>	P	ES, Bp, Lp, V, C	Ob-X	Ax	ES	Burrows (2000)
Myrtaceae	<i>Eucalyptus</i>	<i>eximia</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>ficifolia</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>globulus</i>	P	ES, Bp, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>lehmannii</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>leucoxydon</i>	P	ES, Bp, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>macrocarpa</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>macrorhyncha</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>melliodora</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>nicholii</i>	P	ES, Bp, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>occidentalis</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>regnans</i>	P	ES, B, C, Lp, V	Ob-C, Ob-X	Ax	ES	Cremer (1972), Waters et al. (2010)
Myrtaceae	<i>Eucalyptus</i>	<i>rossii</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>sideroxydon</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	spp.		ES, Bp	B-X		ES	Burrows et al. (2010)
Myrtaceae	<i>Eucalyptus</i>	<i>torquata</i>	P	ES, C	Ob-X	Ax	ES	Burrows (2002)
Myrtaceae	<i>Eucalyptus</i>	<i>viminalis</i>	P	ES, B	Ob-C	Ax	ES	Cremer (1972)
Myrtaceae	<i>Lophostemon</i>	<i>confertus</i>	P	M, Bp, Lp, V	Ob	Ax	EC?	Burrows (2002)
Myrtaceae	<i>Lophostemon</i>	<i>lactiflorus</i>		B, Bp	Ob		EC?	Burrows et al. (2010)
Myrtaceae	<i>Melaleuca</i>	<i>nervosa</i>		Bp, ES	lb		EC?	Burrows et al. (2010)
Myrtaceae	<i>Melaleuca</i>	<i>viridiflora</i>		Bp, ES	Mb-lb		EC?	Burrows et al. (2010)
Myrtaceae	<i>Osbornia</i>	<i>octodonta</i>	N					Burrows et al. (2010)
Myrtaceae	<i>Stockwellia</i>	<i>quadrifida</i>		ES, Bp	Ob-lb		ES?	Burrows et al. (2010)
Myrtaceae	<i>Syncarpia</i>	spp.	P	ES, C	Ob-X	Ax	ES	Burrows (2008)
Myrtaceae	<i>Syzygium</i>	spp.	P	ES, B	Ob-lb		EC?	Burrows et al. (2010)
Myrtaceae	<i>Tristaniopsis</i>	spp.	P	ES, C	Ob-X	Ax	ES	Burrows (2008)
Myrtaceae	<i>Xanthostemon</i>	<i>paradoxus</i>		Bp	Mb		EC?	Burrows et al. (2010)
Oleaceae	<i>Fraxinus</i>	<i>excelsior</i>	A, P	B, Lp, V	P, B, Ob-lb	Ax, Ad	IB	Fink (1908a, 1908b, 1983)
Rhizophoraceae	<i>Rhizophora</i>	<i>mangle</i>	A*, P	M, Lp	Ob	Ax, Ad	IB?	Gill and Tomlinson (1971)
Salicaceae	<i>Salix</i>	<i>alba</i>	P	M, Lp, V	Ob	Ax	EC	Fink (1980a, 1983)
Salicaceae	<i>Salix</i>	<i>amygdaloides</i>	P	B, Bp, C, Lp, V	B	Ax	IB	Sennerby-Forsse and Zsuffa (1995)
Salicaceae	<i>Salix</i>	<i>eriocephala</i>	P	B, Bp, C, Lp, V	B	Ax	IB	Sennerby-Forsse and Zsuffa (1995)
Salicaceae	<i>Salix</i>	<i>viminalis</i>	P	B, Bp, C, Lp, V	B	Ax	IB	Sennerby-Forsse and Zsuffa (1995)
Tiliaceae	<i>Tilia</i>	<i>platophyllos</i>	A, P	B, Lp, V	B, C	Ad, Ax	IB	Fink (1980b, 1983)
Ulmaceae	<i>Ulmus</i>	<i>carpinifolia</i>	A	M		Ad	IB	Fink (1980b)

- ¹ P, preventitious; A, adventitious; N, no epicormics; *classification stated by study author but not verified with morphological evidence.
- ² B, developed buds; Bp, bud primordia; Bs, bud scales; C, cambium or procambium; DM, detached meristem; ES, epicormic strand; Lp, leaf primordia; M, meristem with no bud-like organization; V, vascular tissue.
- ³ B: bole surface; Ob, outer bark; Mb, mid bark; Ib, inner bark; C, cambium; Co, cortex; P, phloem; Ph, pheloderm; X, xylem. Hyphenated cells indicate that the epicormic structure occurs anywhere between the two identified locations.
- ⁴ Ax: leaf axil (includes accessory buds); Ad, adventitious; Bs, bud scale axil; La, lateral bud; L, lenticel; Co, collateral bud; *classification stated by study author but not verified with morphological evidence.
- ⁵ EC, external clustering; IB, isolated bud; DM, detached meristem; ES, epicormic strand; ?, insufficient data to clearly assign epicormic strategy.

2000, Burrows et al. 2010, Waters et al. 2010), especially the eucalypts, which show that this family has developed unusual sprout-producing meristems. Eucalypt epicormic structures consist of meristem strands within the bark that are capable of continuous bud production for a long period of time (Cremer 1972, Burrows 2002). Referred to as a 'persistent axillary meristem' (Cremer 1972), an 'epicormic strand' or 'epicormic meristem strand' (Burrows 2002), or 'meristem strips' (Crisp et al. 2011), these strands are largest near the vascular cambium, but may be present from near the bole surface to the depth of the outer xylem (Burrows 2002, 2008, Burrows et al. 2010, Waters et al. 2010; see Crisp et al. (2011) for a definition of types under this strategy based on the depth of bud-forming cells within the bark). Epicormic strands in older shoots are larger than those in newly formed shoots, a consequence of continued development over time (Burrows 2000); these strands may persist for the entire life of the tree. Fully developed buds do not form without an external stimulus, mainly thought to be fire (Burrows 2002, Waters et al. 2010, Crisp et al. 2011). The epicormic strand structure is widely conserved in the eucalypts and other closely related genera (Burrows 2002, 2008, Burrows et al. 2010, Crisp et al. 2011), occurring even in *Eucalyptus regnans* F. Muell. which is considered to be a non-sprouting species (Waters et al. 2010).

Factors contributing to epicormic bud dormancy release

Stress

Epicormic sprouting is basically a tree's response to stress (Stone and Stone 1943, Burrows 2008). Some stressors are obvious, such as insect defoliation (Piene and Eveleigh 1996), fire (Burrows 2008), frost (Bégin and Filion 1999), wind damage (Cooper-Ellis et al. 1999) or disease (Lanner and Bryan 1981). Others may not be immediately apparent. Drought (Burrows 2002), intense competition (Nicolini et al. 2001), low site quality (Mujuri and Demchik 2009), bole orientation (Della-Bianca 1972, Deal et al. 2003) and vascular embolisms (Nicolini et al. 2001) have also been cited as factors that stimulate epicormic bud sprouting. Most of these stressors result in leaf area reductions or inefficiencies that in turn limit growth rates, necessitating a mechanism for re-establishment or maintenance of a functional and effective crown (Deal et al. 2003).

Tree vigor

There are many silvicultural and ecological studies that implicate tree vigor as playing a major role in the tendency of trees to produce epicormic sprouts, with less vigorous trees bearing more epicormics (O'Hara and Valappil 2000, Nicolini et al.

2001, 2003, Deal et al. 2003, Miller and Stringer 2004, Colin et al. 2008). Treatments such as pruning reduce vigor by removing leaf area; heavy pruning has been shown to be a significant promoter of epicormic sprouting (O'Hara et al. 2008, O'Hara and Berrill 2009). Silvicultural studies often assess vigor in terms of traditional crown classes (Smith et al. 1997) and have most often found that intermediate and overtopped trees are more susceptible to epicormic branching than dominant and codominant trees (Figure 3) (Smith 1965, Erdmann et al. 1985, Johnson et al. 1998), though even dominant trees are capable of producing a large number of epicormic branches (Harmer 1992, Strong and Erdmann 2000). Large-diameter trees also tend to have fewer epicormic branches (Miller and Stringer 2004), but, again, this is not always the case (Auchmoody 1972). Much of the inconsistency regarding the association between tree vigor and epicormic branches is related to the fact that measured variables may not directly quantify vigor, and because current stand conditions may not reflect those in the past. Crown class is probably a poor predictor because it is only an indicator of relative stand structure; codominant trees in a pole-sized plantation are often of only intermediate vigor because their growth is restricted by intense competition. Relationships between tree diameter and epicormics may be confounded by previous stand dynamics; a simple measure of tree diameter is unable to account for past suppression. Vigor indicators that track growth, such as diameter increment (Nicolini et al. 2001) or volume increment (Colin et al. 2008) have proven to be more effective predictors of epicormic sprout formation.

Light

Increased light has historically been considered a primary factor influencing the release of epicormic buds from dormancy, especially in the context of forest management (Blum 1963, Smith 1965). Photochemical reactions with plant hormones have been proposed as the main mechanism whereby auxin inhibition is removed from epicormic buds (Bernsten 1961, Roussel 1978). Some empirical evidence backs this assumption, though little research has directly tested this phenomenon and, as will be discussed later, hormonal control over bud sprouting is more complex than simple auxin inhibition. Although some studies have shown that stem shading limits bud sprouting (Vogt and Cox 1970, Gordon et al. 2006), others are inconclusive (Wilson 1979, Wignall and Browning 1988a, Spiecker 1991).

Evidence that light is not the primary factor stimulating epicormic bud dormancy release is prevalent in natural stands, where for some species, epicormic branches are common in completely closed, undisturbed forests (Herman 1964, Harmer 1992, Nicolini et al. 2001). For those epicormic branches that do sprout, both persistence and growth clearly increase following increases in available light (Wignall and Browning 1988a, Spiecker 1991, Yokoi and Yamaguchi 1996, Deal et al. 2003). Before any definitive conclusion can be made about the impacts of light, however, more information is needed on the physiological mechanisms by which light influences the sprouting of epicormic buds and whether light sensing mechanisms in the canopy are able to signal bud release lower on the bole.

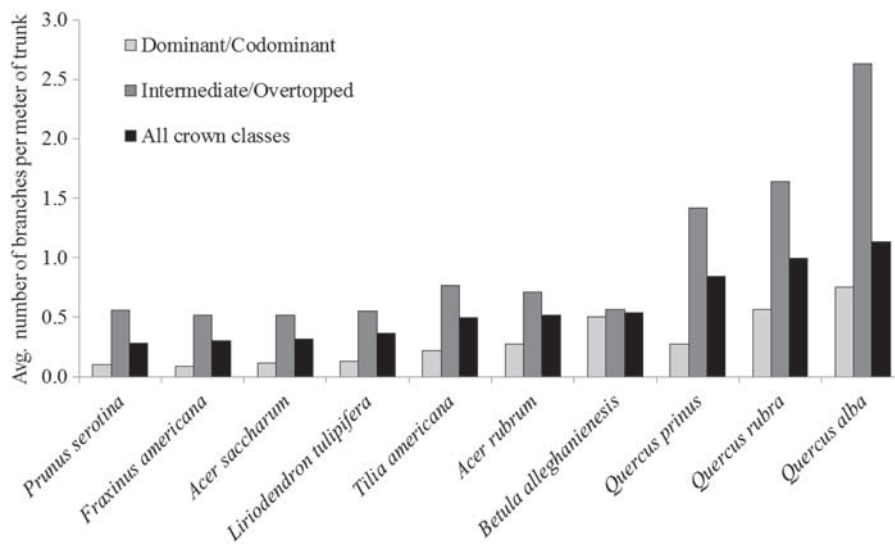


Figure 3. Average number of epicormic branches per meter of trunk below 9.8 m for common North American hardwoods of various ages and silvicultural treatments, stratified by crown class. All included studies counted epicormics around the entire circumference of the bole. Data from: Auchmoody (1972), Della-Bianca (1972), Erdmann and Peterson (1972), Erdmann et al. (1985), Johnson et al. (1998), Miller and Stringer (2004) and Smith (1965, 1977).

Tree architecture

It has been clearly shown that epicormic branching is important for maintaining aging crowns and for maximizing light interception in conifers (Bryan and Lanner 1981, Gruber 1994, Ishii and Ford 2001) and hardwoods (Remphrey and Davidson 1992, Del Tredici 2001, Vesk and Westoby 2004), a process known as delayed reiteration (Ishii et al. 2007). Buds in proximal positions on old, long branches or old, tall trees may enable a more efficient hydraulic pathway for water, nutrient and photosynthate transport (Ishii et al. 2007). Epicormic sprouts in these areas may be 'parts of the tree where photosynthate can be more profitably invested' (Sprugel 2002) and may become more competitive for resources in comparison with more distal meristems. Sprouting occurs both to replace senescing or damaged terminal shoots (Remphrey and Davidson 1992, Wilson and Kelty 1994) and to provide local sinks for retranslocation of compounds from those shoots (Ishii et al. 2007).

Forest management studies have shown that the number of epicormic sprouts that form on the trunk following silvicultural treatments, such as thinnings or partial retention harvests, tends to be higher in the upper parts of the bole, near the live crown (Erdmann et al. 1985, O'Hara and Berrill 2009, Colin et al. 2010b). Within the crown, epicormic branches sprout with greater frequency from buds closer to the terminal of a parent shoot rather than from its base or throughout the tree, while buds near the crown's periphery are more likely to sprout than those in the interior of or below the live crown (Harmer 1991, Remphrey et al. 2002). Buds nearer to the crown are more likely to be in a position to capture light in the event of crown damage (Nicolini et al. 2001), so it is intuitive that the purpose of epicormic buds is to rebuild the crown, whether in response to damage or to physiological inefficiency. Epicormic branching is, therefore, a normal and integral part of architectural development (Herman 1964, Kormanik and Brown 1969, Bryan and Lanner 1981, Ishii and Ford 2001, Van Pelt and Sillett 2008).

Bud size and persistence

In the absence of disturbance, greater epicormic bud activity with proximity to the live crown and within the crown is probably related to the meristematic development and age of individual buds. Some speculation points to the fact that the sprouting potential of epicormic buds increases with the level of internal development (Wilson 1979, Wignall and Browning 1988b, Harmer 1990, Burrows et al. 2003). Internal development is, in turn, positively correlated with bud size (Gill 1971, Remphrey and Davidson 1994, Fontaine et al. 1999, Lauri et al. 2008). Large epicormic buds, therefore, are more likely to sprout than small ones (Braham and Kellison 1987).

Young sequential and epicormic buds and buds on young stem sections are also more likely to sprout, as opposed to older buds on older stem sections (Kormanik and Brown 1969, Wilson and Kelty 1994, Ishii and Ford 2001, Colin et al. 2010b). When large, highly developed sequential buds do not sprout, however, they abscise sooner than very small buds of the same age (Harmer 1991, Fontaine et al. 2001). Therefore, epicormic buds that are able to persist for many years tend to be small and contain few differentiated tissues, such as leaf or bud scale primordia (Gruber 1994, Sennerby-Forsse and Zsuffa 1995, Fontaine et al. 1998).

The level of internal bud development may be a key difference between tree species considered to be highly susceptible to epicormic branch formation and those that are not. Conifers, which in general produce fewer epicormic sprouts on the bole (Büsgen and Münch 1929, Bond and Midgley 2001, Del Tredici 2001), most often fall in the IB or DM epicormic strategies, with most persistent epicormics either buried in the bark and containing only rudimentary bud scales or with detached meristems. Internal development of both of these meristem types is low and a significant stressor is needed to initiate sprouting. On the other hand, species that most frequently produce epicormic sprouts with comparatively minimal stimulus occur in the EC epicormic strategy, with epicormic buds that extend annually and contain at least a meristem protected by scales and sometimes leaf and bud primordia (Fink 1980a, Fontaine et al. 1998). The more developed organs in these buds may promote bud sprouting and explain why these species have much more complex epicormic structures. Epicormic persistence in the EC strategy probably is facilitated most by the regular sprouting and partial dormancy release of individual buds, resulting in complex clusters, while persistence in the IB strategy is dependent on minimal activity of relatively undeveloped meristems buried in the bark.

Sprouting probabilities, however, decrease as stems age and become larger (Putz and Brokaw 1989, Weigel and Peng 2002). Reasons for this decline are not understood (Vesk 2006, Waters et al. 2010). Thicker bark in older trees may prevent the eruption of buds from epicormic strands or buried buds (Putz and Brokaw 1989, Burrows 2002). Small external buds in EC species may be abscised during bark formation, eliminating their epicormic potential (Smith 1967, Braham and Kellison 1987, Fontaine et al. 2001, Colin et al. 2010c). Alternatively, the assumption that epicormic shoots are ontogenetically juvenile (Fink 1999, Del Tredici 2001) may not be entirely accurate (Cameron and Sani 1994). If older epicormic buds have undergone some level of maturation, could that also decrease their sprouting and persistence potential? The question of whether bud longevity is limited by physiological or physical constraints is yet to be answered.

Hormonal control of epicormic bud dormancy

Epicormic buds and dormancy stages

The developmental variation between epicormic and sequential buds suggests that there are differences in physiological control between them (Church and Godman 1966). Annual dormancy of regular buds in most temperate perennial plants is thought to be moderated by the environment (ecodormancy), plant structures external to the bud (paradormancy) and the physiology of the bud itself (endodormancy; Lang 1987). Transitions between dormancy stages and active growth are regulated by genetic and hormonal signals within the plant. The process of dormancy release occurs in multiple stages, beginning with the accumulation of chilling temperatures followed by the synthesis of plant compounds and initial bud swelling. Finally, hormonal activity and activation of the cell cycle initiate cell division and stem elongation (Saure 1985, Pallardy 2008). Any buds appearing to remain dormant at this point are under the influence of other plant structures (i.e., paradormancy). If inhibition is not overcome, buds will cycle back into endodormancy without sprouting (Rohde et al. 2000).

Epicormic buds are probably subject to endo- and ecodormancy in the same way that sequential buds are (Wilson 1979, Rohde et al. 2000), because when epicormic budburst does occur, it is generally at the same time as (Church and Godman 1966, Wignall et al. 1987, Wignall and Browning 1988a) or only slightly after (Harmer 1990, 1991) that of sequential buds. Since epicormic structures develop slightly each year, control of epicormic sprouting most likely occurs following the initiation of cell division but before complete shoot elongation. At this time, vigorous shoots in other parts of the tree are able to reassert dominance, causing epicormic buds to enter a paradormant state (Figure 4). Auxins and cytokinins are the most studied hormones associated with dormancy control (Sachs and Thimann 1967, Brown 1971, Rohde et al. 2000) and recent research continues to validate their importance (Tworowski et al. 2006, Rasmussen et al. 2009, 2010).

Auxins

The control of epicormic branching has long been attributed to auxin production in dominant meristems that limits sprouting and development of subordinate buds (Kormanik and Brown 1969, Kauppi et al. 1987, Burrows 1989, Gruber 1994, Wilson and Kelty 1994). Artificial auxin applications, following the removal of a terminal bud, are able to effectively replace the inhibitive action of that terminal on other sequential (Sachs and Thimann 1967, Cremer 1972, Cline 2000) and epicormic buds (Bowersox and Ward 1968, House et al. 1998). Silvicultural treatments that interrupt auxin flow from terminal buds, such as pruning (Kormanik and Brown 1969) or girdling (Wignall et al. 1987), often stimulate epicormic bud sprouting,

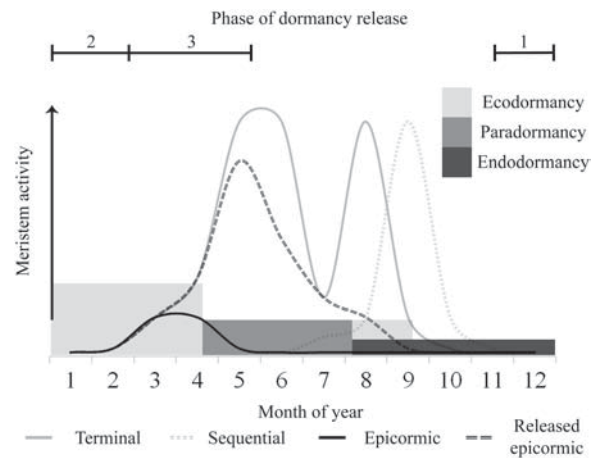


Figure 4. Theoretical schematic of bud activity in a terminal, sequential, unreleased epicormic and released epicormic meristem on a single tree according to the dormancy framework of Lang (1987) and the dormancy release phases of Saure (1985). Lines on the graph represent changes in bud activity. Shaded boxes delineate periods when buds are under the control of the associated dormancy type. Height of the shaded boxes corresponds to the amount of meristem activity that may potentially occur within a given dormancy type without complete dormancy release. When lines are not within a shaded box, the bud is actively growing. Brackets on the top of the graph represent the phase of dormancy release associated with stages of bud dormancy. Bud activity in months 8 and 9 represents a second flush of the terminal bud followed by release of a subtending sequential bud.

suggesting that the loss of an auxin source enables bud dormancy release.

Leaf primordia and young leaves in expanding buds are important sources of auxin in growing shoots (Aloni et al. 2003). These auxins move downward in the tree through basipetal transport (Wignall et al. 1987, Sundberg and Uggla 1998) and preclude the further development of other buds lower in the tree (Sachs and Thimann 1967, Kauppi et al. 1987). Within individual branches, increasing distance from the apex is correlated with increased auxin concentrations (Alden 1971). Although it has not been experimentally demonstrated, it seems intuitive that the auxin concentration at the base of a tree would be a function of the total auxin production of all branches above that point. Auxin inhibition, therefore, probably increases with distance from the apical meristem, since buds at the base of a tree would be suppressed by auxins transported from all the buds on the tree (Rasmussen et al. 2010).

However, epicormic bud control is almost certainly more complex than simple auxin inhibition (Sachs and Thimann 1967, Kormanik and Brown 1969, Wignall and Browning 1988b). Both epicormic and sequential branches form at a time when growth of terminal shoots is most rapid, and therefore when auxin concentrations in the tree are highest (Wignall and Browning 1988a, Cline and Dong-Il 2002). In some cases, other compounds can inhibit bud growth just as effectively as auxin (Bachelard 1969), while endogenous auxin production

within the inhibited buds actually promotes growth (Sachs and Thimann 1967). Instead, dormancy control is moderated by the interaction of auxin with other plant hormones, especially cytokinins, and environmental factors (Wilson 1979, Kauppi et al. 1987, Cline and Dong-Il 2002, Tworkoski et al. 2006).

Cytokinins

In buds, cytokinins are most often considered to be important in regulating both cell division and elongation (Chen et al. 1996, Shimizu-Sato and Mori 2001, Pallardy 2008, Davies 2010), and are generally classified as promoters of sprouting (Sachs and Thimann 1967, Wignall and Browning 1988b, Cline and Dong-Il 2002, Ongaro and Leyser 2008). However, no studies have directly assessed cytokinin levels in epicormic buds; therefore, much of the following has been drawn from studies on sequential buds. The influence of cytokinins on bud-burst has most often been characterized as a direct interaction with auxins; when cytokinin concentrations at the bud are high relative to auxins, the bud is able to sprout (Brown et al. 1967, Sachs and Thimann 1967, Brown 1971, Shimizu-Sato and Mori 2001, Cline and Dong-Il 2002, Tworkoski et al. 2006). The cytokinins required to overcome auxin inhibition have been thought to be transported acropetally from the roots to the bud (Fink 1999, Tworkoski et al. 2006). However, there is evidence that the cytokinins that stimulate bud growth are synthesized in tissues immediately below the buds and that movement of cytokinins from the roots is minimal (Wignall and Browning 1988b, Rasmussen et al. 2009, 2010). It has also been proposed that cytokinins do not promote sprouting but instead promote growth following dormancy release (Pallardy 2008).

It is now apparent that the auxin to cytokinin ratio at the time of sprouting may not be the only hormone interaction that allows a bud to overcome inhibition (Bollmark et al. 1995). Instead, the role of cytokinins is also important at the time of bud formation since, as buds are established, cytokinin levels are positively correlated with resting bud size and internal development (Bollmark et al. 1995, Chen et al. 1996), and both increased bud size and development subsequently increase the probability that a bud will sprout (Gill 1971, Cochard et al. 2005). Much of the critical cytokinin activity, therefore, occurs in the growing season before sprouting (Chen et al. 1996). Reported insensitivity to high auxin to cytokinin ratios in association with high nutrient availability (Tworkoski et al. 2006) may instead be a reflection of greater bud development in the previous growing season.

New signaling pathways in herbaceous plants

Major advances have been made in the last decade to detail the complex pathways and signals involved in axillary bud paradormancy control in model herbaceous plant systems. Inconsistencies in the basic premise that auxin and cytokinin dynamics alone are responsible for the outgrowth of

paradormant axillary buds led to the identification of a novel group of hormones, the strigolactones, that are involved in long-distance auxin communication (see Dun et al. 2009 and references therein). The signaling pathway in which strigolactones play an important role, now known as the MAX/RMS/D pathway, is yet to be completely described (Beveridge and Kyojuka 2010), but it appears that a feedback cycle occurs in which strigolactones moderate auxin levels and vice versa (Hayward et al. 2009, Beveridge and Kyojuka 2010), while the activity of auxins controls cytokinin synthesis to some extent (Ongaro and Leyser 2008, Beveridge and Kyojuka 2010). Strigolactones have not yet been described in woody plants, but, considering the fact that the MAX/RMS/D pathway is mainly associated with paradormant release, the same state of dormancy as in epicormic buds, it seems likely that some form of this pathway may be active in woody plants as well. Champagnat (1989) proposed that both long-distance and short-distance inhibitors were present in woody plants; the MAX/RMS/D pathway appears to fit well into the idea of a short-distance inhibitor.

Relationship between hormones and nutrient dynamics

Although there is significant evidence for hormonal control of epicormic branching, how do hormones interact with other aspects of plant growth, especially nutrient dynamics? The ability of the growing shoot to take up nutrients is correlated to the initial bud size, and this is correlated with both auxin and cytokinin levels (Little 1970, Bollmark et al. 1995), possibly because of higher xylem conductivity associated with larger buds (Wignall and Browning 1988b, Cochard et al. 2005). Xylem conductivity may be moderated by the stimulative effect of auxin production in the bud on vascular differentiation (Aloni 2010). Therefore, small buds are likely weak nutrient sinks that are not competitive when nutrients are limiting. In young shoots, there is solid evidence of greater bud activity at high nutrient levels (Kormanik and Brown 1969, Little 1970, Harmer 1989). In older trees, little response (Auchmoody 1972) or even a reduction in epicormic branching (Geyer et al. 1979) has been noted at high nutrient levels. This apparent contradiction may be due to the fact that the studies in older trees assessed only buds on tree boles, which were probably smaller and less competitive for nutrients. It may be that if these studies had assessed bud dynamics in the crowns, their findings would have been different.

Carbon allocation during annual flushing in temperate trees is another important nutrient dynamic that may influence the tendency of epicormic buds to sprout. Irrespective of the hormonal and regulatory influences on prior development of a structure, carbon allocation is thought to be driven mainly by the relative strength or weakness of carbon sinks (areas that are net carbohydrate importers) the vascular network in place to transport carbohydrate and the proximity of carbon sources

(areas which are net carbohydrate exporters). The potential growth rate of buds may be used to quantify sink strength; large sequential buds are very strong carbohydrate sinks, while small buds can be very weak (Smith 1967, Little 1970, Kozlowski 1992). With this in mind, a small epicormic bud low on the bole of a tree with minimal vascular development would be a weak carbon sink relative to the strong sink activity of rapidly expanding shoots from large sequential buds in the crown (Dickson et al. 2000). By the time vigorous sequential buds form leaves that become net exporters of carbohydrates, hormone production by the vigorous shoot could take over and cause complete cessation of growth in the epicormic buds.

Budburst dynamics in response to decapitation treatments suggest that, in response to stress, signaling pathways and not carbon allocation dictate bud dormancy release. When terminal buds were removed in temperate tree seedlings at the beginning of the spring flush, the uppermost sequential buds remaining following decapitation were the only ones that were released (Cline 2000). If carbon allocation was driving dormancy release, release should have corresponded to bud size without regard to stem location. According to speculation by Dun et al. (2009) in herbaceous plants, the slow movement of auxin through the stem, coupled with the activity of other signals (possibly strigolactones), causes apically produced auxins to decline at the most distal point on the plant first, thus removing inhibition of those buds. As those buds begin to grow, they synthesize auxin, which is transported down the stem to replace the repressive effects of auxin lacking after removal of the terminal. Strigolactones at this point may act as temporary hormonal control in lower buds in the period of time between loss of dominance from the lost terminal and establishment of dominance from newly sprouted lateral buds.

A distinction should be made at this point between epicormic sprouting stimulated by significant stress, such as loss of a terminal bud or fire, and that stimulated by unobserved physiological interactions within the tree. Genes related to stress are upregulated following decapitation (Liu et al. 2011), and since the ecological objective of resprouting following disturbance is to rapidly recover lost growing space (Bégin and Filion 1999, Bellingham and Sparrow 2000), rapid shoot regeneration from the highest point on the stem is critical. However, when significant stress is absent, normal shoot growth dynamics probably regulate epicormic sprouting. Therefore, though decapitation studies provide useful insights into hormone dynamics, they cannot be separated from a co-occurring stress response. We propose that bud size and internal development are critical factors allowing epicormic buds to overcome auxin inhibition in the absence of disturbance, while sprouting in response to stress is initiated via stress-activated signaling pathways. This dichotomy explains why species in the EC strategy readily

sprout without disturbance, while species in the other strategies rarely sprout except in response to stress.

Genetics

Cell-level genetic control

We are aware of only two studies that have considered paradormancy release at the molecular level in woody plants (Brunel et al. 2002, Liu et al. 2011). A comparison of one sprouting and one non-sprouting *Pinus* species showed a number of differentially expressed genes following top removal; many of these were associated with stress response, cell growth and protein metabolism. A few hormone-related genes were also identified (Liu et al. 2011). One gene of particular interest was noted, an upregulated transcriptional regulator in the *Arabidopsis* Knotted1-like homeobox gene family. A similar gene was reported in *Malus domestica* [L.] Borkh. (Rosaceae) that has been categorized as a potential inhibitor of budburst in spring (Brunel et al. 2002). Further study of this gene family in relation to sprouting would be merited. A number of other studies have assessed the molecular characteristics of ecodormancy release in the sequential buds of other tree species (Frewen et al. 2000, Jermstad et al. 2001, Scotti-Saintagne et al. 2004, Casasoli et al. 2006). Although many genes associated with bud growth following release may be similar between ecodormant and paradormant buds, the critical genes that actually trigger budbreak are probably different.

Quantitative genetics

The number of epicormic branches that form on an individual tree has been thought to be under some level of genetic control for some time (Ward 1966, Bryan and Lanner 1981, Remphrey and Davidson 1992, O'Hara and Valappil 2000). Little empirical evidence is available to verify this; there do appear to be some clonal differences in epicormic branching (Bowersox and Ward 1968, Kuser and Knezick 1985, O'Hara and Berrill 2009), but provenance level differences are minimally important (Colin et al. 2010a). Most of these studies have assessed the total number of epicormic branches at a given time, even though it is not clear that a single estimate of epicormic branch numbers is the best trait to characterize the influence of genetics on epicormic dynamics since the interaction of genetics and the environment may lead to unpredictable fluctuations in epicormic branch numbers over time.

Specific heritability estimates for epicormic branching are rare. This is somewhat surprising considering that both the economic importance of epicormic branches and the common perception that epicormic tendencies are heritable. In teak (*Tectona grandis* Linn. f., Verbenaceae), heritability of epicormic branching in a single study was quite low: 0.03 for narrow-sense and 0.12 for broad-sense heritability (Callister and

Collins 2008). For *Quercus* spp., a much wider range of heritabilities has been reported, from 0.38 to 0.57 for *Quercus robur* L. and *Q. petraea* (Savill and Kanowski 1993, Jensen et al. 1997). Provenance level heritability was much lower in these studies. Others (Chen et al. 1995, Jensen 2000, Callister and Collins 2008) found similar variation in heritability estimates, which presents evidence that differences in site and environment play a significant role in epicormic branch production. Some variation in these estimates could also be explained by differences in assessment techniques. In most cases, epicormic structures other than epicormic branches were not counted. These heritability estimates were also based on qualitative measures of branching relative to other trees within a site; whether these qualitative assessments can be compared among different species, studies, tree ages, or even between sites in a single study, can legitimately be questioned.

It is surprising that only a few authors have actually considered which epicormic trait has the greatest selection potential and when that trait should be considered. For oaks, selections should be based on the number of complex, developed epicormic structures on the bole rather than on the number of branches (Colin et al. 2010a, Morisset et al. 2012b), since the number of sprouted epicormic branches fluctuates widely over time (Morisset et al. 2012b). There is some consensus that epicormic structures are most active and under the least physiological control in young trees (Kormanik and Brown 1969, Ishii and Ford 2001, Colin et al. 2010b), and that the number of epicormic structures present at very small shoot diameters is a strong predictor of the number of epicormic structures in large trees (Morisset et al. 2012b). Therefore, identification of superior phenotypes is probably most effective when trees are relatively young (Kormanik and Brown 1969, Morisset et al. 2012b).

Synthesis

We propose the following generalizations to explain differences among woody plant genera in the establishment, development and sprouting of epicormic buds. The primary driver of interspecies variation in epicormic sprouting occurs as a result of fundamental developmental differences. Annual shoot growth within an individual species is highly regulated; therefore, the proportion of large, reactive primary buds to small, persistent buds is indicative of long-term epicormic dynamics. Species with more large buds form sprouts early in life but quickly lose epicormic potential, while those with persistent buds and meristems maintain epicormic potential for decades. Environmental and genetic variation among individuals within a species further influences the number of primary buds that initially develop, mainly as a function of the number of buds per unit of length on a shoot.

Following the establishment of primary buds, ontogenetic pathways and physiological parameters begin to play a more

important role. A critical step in the development of epicormic potential is the transition from a dormant primary bud on a leafy annual shoot to an epicormic bud or meristem on an older shoot. At this point, interspecific variation in both ontogeny and physiology is the most important determinant of epicormic potential. The probability that a bud will persist as an epicormic bud is a function of its initial size and developmental status. Large buds are more likely to sprout or die, while small buds are more likely to remain dormant. Death of a bud generally decreases the epicormic potential of a tree, while sprout formation may increase the epicormic potential through the addition of new buds. Therefore, genetic and environmental determinants of the number of buds established cede prominence to physiological and ontogenetic processes that influence bud mortality and persistence in the period between bud establishment and sprouting. Trade-offs between epicormic bud development and persistence mean that as stems age and fail to produce sprouts, the surviving buds are those which require the greatest stimulus to sprout. On very old stems, initial epicormic buds reach a stage beyond which they are not able to sprout and the epicormic potential of the bole becomes negligible.

Bud sprouting is the most complex of these processes and is the least understood. Clearly, epicormic sprouting is a function of environmental inputs, but the regulatory pathways that respond to environmental cues have not been explained. We propose that epicormic bud sprouting is ultimately a response to a physiological imbalance in the tree crown that necessitates an expansion of leaf area to either increase the likelihood of tree survival (Nicolini et al. 2001) or to maximize its capture of resources (Ishii and Ford 2001, Sprugel 2002, Deal et al. 2003, Ishii et al. 2007). Plant hormones play a critical role in signaling the tree's response; though there may be genetic differences in the effectiveness of signaling pathways (Ongaro and Leyser 2008) or in bud sensitivity to hormones (Cline and Dong-Il 2002). With a large number of processes involved in bud dormancy control, bud break is necessarily dependent on a large number of genes. Variation in these genes among individuals within a species is expressed phenotypically as variation in the number of sprouted epicormic branches present at a given time. Control over bud dormancy is moderated by auxin production in the crown and the state of development of individual buds and meristems. The size and internal development of a bud is in turn associated with cytokinin production at the time of bud formation. Large buds are also stronger carbohydrate sinks at the time of bud sprouting, indicating a complex interaction between bud vigor and auxin production in the tree crown and auxin inhibition lower on the stem. Damage to terminal shoots initiates a stress response that stimulates sprouting of buds nearest to the damage, while without significant damage, the location of sprouts is related to bud development. Since buds in the youngest parts of the tree are most often

also the largest, epicormic branch formation increases with height on the tree. The influence of light on epicormic sprouting is not certain; however, newly formed branches are much more vigorous in high light environments.

Future directions

There are a few key basic research needs to increase our understanding of epicormic bud development and sprouting. Further anatomical and ontogenetic studies are needed for a wider variety of species. No comprehensive model of epicormic bud dynamics can be proposed when the epicormic strategies of most species are not well known.

Detailed physiological studies of epicormic bud dynamics are lacking and the basic physiology of epicormic bud dormancy control has not been well described. Comparisons of the impacts of nutrient, water and hormone dynamics on the sprouting potential of epicormic buds of different sizes and from different species are needed. The hypothesis that a stress response stimulates different sprouting dynamics in decapitated versus intact trees should also be tested; if this is the case, different methods of control may be warranted to prevent epicormic branching in high-value timber stands.

The identification of some genes and transcripts responsible for epicormic sprouting would help to clarify both the level of genetic variability in epicormic control and which epicormic traits are the most critical determinants of epicormic bud dynamics. Quantitative trait loci mapping and cDNA analysis focused on epicormic buds in species where this work has already been done for sequential buds could be informative. The potential for using the extensive base of genomic data available for *Populus* (Jansson and Douglas 2007) may also provide an opportunity to assess whether novel axillary bud control pathways in herbaceous plants have an analog in trees; such a discovery would greatly enhance our understanding of the molecular and physiological controls of epicormic buds in trees.

In the field of forest genetics and tree breeding, it is paramount to identify both the best time and the best method for selection of phenotypes that are less susceptible to epicormic branching. An initial step in this process would be the development of a more objective, quantitative method for rating epicormic branches that could be applicable across most species. Subjective, rating-based methods are difficult to compare between species and sites, especially when rating is undertaken by different individuals. The previously proposed studies emphasizing epicormic ontogeny will be helpful in identifying which structures to quantify and at what developmental stage trees are most likely to clearly display their epicormic potential.

Finally, silvicultural studies are needed that emphasize the response of buds to forest management activities, rather than

focusing exclusively on the difference in branch numbers prior to and following cultural treatments. Long-term studies should be installed that track the development of epicormic structures over time in response to different thinning and release treatments at various stand ages and for species with contrasting epicormic strategies. Studies that only consider epicormics for a few years prior to and a few years after a treatment almost certainly do not encapsulate all the factors that influence epicormic formation.

Conclusions

The production of epicormic meristems is a trait that is highly conserved among tree species around the globe as a mechanism to either reestablish leaf area following a disturbance (Bellingham and Sparrow 2000, Crisp et al. 2011) or to maximize light capture in the absence of disturbance (Nicolini et al. 2001). There is significant diversity in the anatomy and morphology of these meristems in tree species; however, much of this diversity can be categorized into four different general epicormic strategies: external clustering, isolated buds, detached meristems and meristem strands. There is a gradient in the level of development of meristems between these strategies which corresponds to a gradient in the likelihood of epicormic sprouting. In the absence of disturbance, epicormic bud sprouting and development is moderated both by plant hormone dynamics and by variation in bud size. Following a severe stress event, such as top removal, trees initiate a stress response that stimulates the growth of much less developed meristems to rapidly replace lost biomass. Therefore, species that do not form sprouts in undisturbed forests but still maintain sprouting capacity most often maintain regenerative meristems in a minimally developed state that are only capable of sprouting with severe disturbance.

However, from the perspective of forest managers and geneticists interested in limiting the impact of epicormic branching on the future value of forest products, important questions still remain. Until recently, both basic and applied research have focused mainly on branch formation subsequent to stand disturbance, while there has been little consideration of the basic factors that influence the establishment of epicormic buds and their maintenance over time. This review has aimed to elucidate some of these factors. We hope that the current resurgence in epicormic research will finally provide answers to many longstanding questions and provide a direction for practical application.

Supplementary data

Supplementary data for this article are available at *Tree Physiology* Online.

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Conflict of interest

None declared.

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