Wind and plants: enemy and friend. A forest perspective

One line, "No rain, no crop, no feed, no faith, only wind" from Anne Marriott's poem *The Wind Our Enemy* tells a vivid story of life on the Canadian Prairies during the dust bowl years. Uprooted trees portrayed the devastation caused by the wicked winds of the 2005 Hurricane Katrina when it hit New Orleans and the Gulf Coast of the United States. On December 15, 2006 a powerful wind made a shocking change in the appearance of the forest in Vancouver's Stanley Park (UBC Faculty of Forestry, 2007). Wind indeed is enemy to plants, but in numberless ways it is also friend, and in the long term is essential in ecosystems.

What is wind?

One dictionary defined wind as "air moving horizontally." How bland! And not quite correct because some winds blow up and some down. Such a definition gives no idea of the diversity of winds; wind is moving air; that may carry water, dust, ice, sand and chemicals. Above all wind has energy that can be transferred to sailing ships and windmills and can be used by plants in ways essential to their growth and development.

Different is the "wet monsoon" wind of India from the dry hot "Mistral" blowing into France from the Sahara, from the "foehn" blowing from the European Alps or from the "Squamish" winds blowing into the fiords of the BC coast from the Interior Plateau. To the ancients, wind was mysterious. Where did it come from and where did it go? In Scandinavian mythology, Thor was the god of the north wind and the god of battle and tempest. Aeolius was the ancient Greek god of the four winds. Today wind has lost much of what the ancients found so intangible but we still feel the "poetic" or "archaic" wind as

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somewhat different from the winds of science, the winds of air mass analysis, the jet stream or the solar wind.

The poetic or archaic wind may be the wind of main interest to the botanist, the naturalist, the artist and photographer; "a modernized poetic wind?" Artists such as the members of the Canadian Group of Seven painted wind as the tatter and flag of trees and the stormy waves of Lake Superior. Ansel Adams famously photographed pines on the rim of the Colorado Grand Canyon and Yosemite cliffs to portray wind. The "poetic" designation in the English vocabulary is rich in words describing the energetic wind; gale, tempest, storm, tornado, cyclone and others and rich in descriptors (adjectives), dry, cold, bitter, ill, mischievous, dusty, etc. Gary Paul Nabham, writing about the famous American pioneer naturalist, scientist, Thoreau, said, "he (Thoreau) saw no polarity between poetry and nature's economy but instead envisioned an ecology that spans both and enriches our senses, beauty and mind".

When does the poetic or archaic wind, become the wind of science, of air mass analysis or the global wind? The distinction is seamless but useful nonetheless and general texts such as those by E.C. Pielou (2001), J. Phillipson (1966), or de Villiers (2006) provide a useful perspective of science and the energetic wind.

Wind and the evolution of plants

When unicellular plants first established on land, wind may have played a role in their dispersal. Once they evolved as multicellular and erect, they have affected and been affected by wind speed and direction. Fossil evidence suggests that by the Silurian, 500 to 700 million years ago, leaf-like structures with stomata and semi-permeability had evolved (de Villiers, 2006) and that the sporophyte generation of the seed plants was large (and the gametophyte generation diminished) and a conducting system with root and stem had evolved. Why the bryophytes with a relatively large leafy gametophyte and a small sporophyte with only rhizoids and a poorly developed conducting system should remain short statured, hugging the ground as the mosses and liverworts do today is not clear from the fossil record. We assume that wind played a role in the evolution of the root as a holdfast and uptake organ for water and soil nutrients, and in evolution of the stem to support leaf and flower. The vascular system provided effective transport between root and shoot to meet the needs of the expanding photosynthetic surfaces. Does wind continue to play a role as one of many factors in the evolu-

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Figure 1. Parallel veined moncot leaves split by high winds, driving hail, or rain. *Veratrum virides* (false hellebore). Trophy Mountains, BC.

Figure 2. Brittle limbs of *Populus trichocarpa* (black cottonwood) broken by wind and ice storms. Nicomen Island, BC.

tion of plants? The internal and external architecture of leaves seem to affect the type of damage caused by high wind. Often the parallel-veined monocot leaves are torn to strips (Figure 1) reticulate-veined dicot leaves are bent at the petiole or broken at the stem insertion.

Wind energy, flex plants and brittle plants

Broken cottonwoods silhouetted against a Fraser Valley sky (Figure 2) attest to the brittleness of old branches in wind and ice storms while nearby the closely related Lombardy poplars gracefully sway unbroken in the wind. The American, Robert Frost in his famous poem, "Birches" recalls from boyhood (as I do) swinging up and down on young and bending birch trees (Figure 3).

Older birch trees are brittle. *Zea mays* (Indian corn) plants in the windy areas produce brace roots (Figure 4), whereas other cereals, grasses and many forbs, such as *Epilobium angustifolium* (fireweed) flatten and lodge in windstorms, but when young become erect again. Grasses have special structures termed pulvini on stem (culm) just below nodes that assist lodged grasses to become erect again (Figure 5).

Young arborescent species, such as *Alnus sinuata* (slide alder) that have been flattened by wind, avalanche or the weight of snowpacks can

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Figure 3. Flex species: bending *Betula occidentalis* (western birch) is ideal for swinging. Louis Creek Valley, BC.
Figure 4. In windy areas prop roots brace the stems of *Zea mays* (Indian corn) against the wind. Ashcroft, BC.
Figure 5. Wind lodged *Avena sativa* (oat) use pulvini that make wind blown plants erect enough to harvest. Dr. Jim Miltimore, Enderby, BC.

Figure 6. In high snowfall subalpine areas, wind triggers slides or wind and snow together bend younger trees of *Alnus sinuata* (slide alder). Spring wind can help the plants untangle and become erect.

often become erect again (Figure 6). Astonishingly the wind helps to untangle and separate members and to assist in the process of re-erection. There is a special charm in the flexible shoots of weeping willows or birches. Landscapers often place them on the margins of lakes and streams providing a curtain of swaying limbs that create a dynamic view across the water.

Wind, waves and aquatic plants

Most aquatic plants are flexible. The energy balances between physical support and transport in land plants that are provided by lignin and cellulose are changed because the water provides much of the physical support for stem and leaf. Some aquatics are submerged and largely out of the direct impact of the buffeting effects of wind and wave but others such as water lilies and pond weeds produce foliage on the water surface or near the surface. The surface foliage of aquatics may serve to calm small wind-driven small wave motion. In the shallow bays of lake margins and in ponds the long petioles and "split" fronds of water lilies or the ribbon-like leaves of the pondweeds absorb the energy of the waves. Other emergents such as the bulrush (*Scirpus* spp.) rely on the round or triangular cross-section of their rigid stems to absorb most of the buffeting of wind and waves. Flexibility is only one of several factors important in the ecology of emergent aquatics; for example, the timing of the emerging first floating leaves of *Zizania palustris* (annual wild rice) and the water regime and depth appears to confine its geographical range to the shallow waters of the Great Lakes region. Once past the critical flex-leaf stage, stiff culms arise above the water surface. The timing of the leaf emergence must match the rise in the spring water levels; if the levels are too high, the first floating leaves die and the emergent wave resistant culms are not produced.

Mankind has, from ancient times used natural fencing of trees and shrubs to reduce the impact of wind on dwellings and on gardens. The use of flexible whips (branches) by coppicing, pleaching and inosculation deserves mention–coppicing to grow and harvest whips, pleaching to interweave whips to make a fence, which when dry becomes strong, and inosculating to link living whips from one tree or shrub to another. In various ways and to varying degrees and times almost all plants flex in wind.

Windthrow, blowdown, windfall and breakage (trees)

Violent wind can cut into a forest like a scythe cutting grass. The ecological effects of blowdown (Figure 7A), windthrow (Figure 7B) and breakage (Figure 7C) of trees by wind differ somewhat. Blowdown leaves patches of tangled trees that are often discernable at a distance. Windthrow of individual trees allows light penetration of the forest canopy and the sun flecks serve to enhance understorey vegetation and seedling growth on decaying "nurse logs". In addition, windthrow mixes litter with mineral soil. Windfall and breakage leave stumps and sloughing bark accumulating at the base of boles. Insects and fungi provide cavities for nesting birds and food for woodpeckers as they decay attack the stumps. Decayed stumps leave mounds of organic matter on

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Figure 7. Blowdown (A), windthrow (B), and breakage (C) have very different ecological impacts in the forest and savannah.

the forest floor creating microhabitat that may favour western hemlock seedlings while nearby mineral soil favours Douglas fir seedlings.

Throughfall and wind as a "cleansing agent"

Wind, rain, frost, snow and ice all contribute to the 'throughfall', of organic materials shed by woody plants (Figure 8). This rain builds the duff and litter (the mor and the mull) on the mineral soil surface. Throughfall occurs in all seasons but varies in amount. The rain of organic matter includes pollen, bud scales, diseased needles and leaves, twigs, insect frass, bark dust, flower parts and whole catkins, and debris from epiphytes (lichens, mistletoe, etc). Wind serves to clean trees and shrubs of old unproductive or diseased materials, removing shade and increasing exposure to the sun's radiant energy . The throughfall from winter storms, including twigs and branches from the high crowns falls on a snowy surface and provides food for wintering deer, elk, moose and even native sheep (Figure 9).

The twigs are nutrient rich but may also be toxic. Much has been written about the decomposition of throughfall and litter (Dickinson and Pugh, 1974), but very little about its function in nature or about the roles of wind.

Photos: Vernon Brink

Fig. 8 As the snowpack thaws to the frozen soil surface, the winter's winds contribute litter that enriches the soil.
Fig. 9. Nutrient rich twigs and branches from the sunny crowns of *Pseudotsuga menziesii* (Douglas fir) break off in high winter snowfall to make browse much prized by native ungulate species.

Natural bonsai – wind training, flag and tatter

As if defying gales and age, trees and shrubs standing on promontories, rocky shores and sand dunes are often dwarfed and have scraggy limbs and twisted boles. Trained by wind their foliage is flagged and tattered. Bonsai art from Japan and China reflects these forms of woody plants. So do the trees in the paintings of the Canadian "Group of Seven" and the photos by Ansel Adams. Bonsai artists in practice pinch leaf and twig to dwarf a tree or shrub and achieve a wind-tattered form. In nature, cold or dry wind, sometimes does the pinching, the pinches remove and kill new twigs and leaves, greatly reducing the opportunities to build carbohydrate food reserves. Sometimes loss of leaf and twig occurs as a result of abrasion by sand or ice or snow crystals and on marine shores by salty spray. Limited mineral nutrient and water supplies can only come from root penetration of cracks in the rocky cliffs or deep root penetration of sand dunes. Desiccation is often a reason for dwarfing but it is likely not that alone.

Throughfall and summer drought

Dry hot wind and cold soil contribute to water stress in plants. Water stresses evidenced in summer leaf fall often escape the attention of photographers, naturalists and the urbanized public. Plants may pay a high energetic price by losing green foliage in summer. Aided by wind, leaf abscission quickly reduces transpiration and water loss. Older and less photosynthetically active leaves drop first. The impact of needle and leaf losses on flower and fruit production and on carbohydrate reserve food in twig, bole and root may continue for several years following summer drought. Leaf fall in summer often goes unnoticed because there is no associated colour and nutrient withdrawal as is characteristic of autumn leaf fall.

Hot dry summer winds contribute to other responses to water stress. Even pubescent plants such as *Antennaria parvifolia* (pussytoes) behave as natural hygrometers when leaves curl during the day reducing transpiration and uncurl by night or during a humid breeze as they regain turgor. Other plants, such as the *Balsamorrhiza sagittata* (balsam root), draw their crowns into the soil, as the leaves curl, dry, become brittle and are soon shredded by wind and the trampling of animals.

Surface, roughness and wind breaks

Even low-growing rosettes and mats reduce wind velocity and create turbulence. Tall trees influence wind velocity in their lee for up to one hundred times their height. In dense forest, wind velocity on the ground may be greatly reduced while the forest canopy is buffeted. The boles of spaced trees create eddies manifested in winter by the development of snow cirques which in turn result in variations in snow depth, snow melt and soil moisture. Snow cirques provide a distinctive micro habitat for plants and animals.

In spring snow patches may linger and summer soil moisture vary over relatively short distances as a result of variations caused by uneven surfaces, drifting snow, and living snow fences that influence the winds of winter.

Firewinds and catastrophe wind

Land plants evolved in the presence of fires and lightning. Fire is nearly universal. It is unique in that it generates its own wind in complex ways with some special ecological responses. Its destructive, sanitizing or renewing actions make it both an ecological enemy and friend.

Wind and the dispersal of plants and plant parts

a. Pollen and spores (aerobiology)

The ancients and many aboriginal peoples had some understanding of the roles of wind pollination and pollen dispersal. In the western world appreciation of wind function was limited until in the 1700's when several studies on pollination were published. By the mid 1800's, Victorians such as Charles Darwin had established that pollination was a noteworthy service in nature.

The fossil record of wind and insect pollination dates back to the mid-Paleozoic time. Today many more plant species are wind pollinated than insect pollinated, although public attention is directed more towards pollination by insects and other animals and to the colourful co-evolution of flowers and insects. Many plant species take advantage of both wind and animal pollination. Wind is reliable and wind is everywhere but pollen must be produced in prodigious quantities and demands the allocation of much of a plant's energy. The direct transfer of pollen from flower to flower by insect or other animal agent is less energy demanding, but insect populations may be limited by the temperature at which insects fly and by their distribution.

Air-dispersed pollen falls by gravity to receptive surfaces in a seemingly haphazard process, but plants have evolved some efficiencies to aid the basic process. Rate of fall varies, as does its buoyancy. Some pollen is winged or variously patterned on the surface. Plant grouping and the timing of foliage production both can modify and even direct pollen fall. As sufferers from pollen allergies know, the release of pollen is temperature and humidity controlled; as a result, pollen release is efficient and timely. Receptive surfaces and structures, such as the cones of conifers or the foliage of jojoba, facilitate the sequestering of airborne pollen. Feathery stigmas like those of grasses "pluck" pollen from passing zephyrs; other stigmas are sticky and hold grains until germination.

The modern literature on pollination received new impetus and direction in the 1960s with the work of Faegri and van der Pijl (1966). Spores from bryophytes and pteridophytes as well as those from fungi and lichens deserve direct consideration as do bacteria, but reviews of this very large literature do not apparently exist, although the case studies are scattered through the journals of microbiology, plant pathology and other disciplines.

B. Other plant parts

Wind may not be as effective a dispersal agent of seeds, fruits and associated plant parts as it is with the generally smaller propagules of some fungi, lichens and bryophytes, some of which may be distributed worldwide (anemachory, authochory etc. (see Faergi and van der Pijl, 1966, for terminology and classification). Dispersal is governed to some extent by the nature of major reproductive structures such as pods or inflorescence: for example, in *Sporobdus cryptandrus* (sand dropseed grass), where the whole mature inflorescence with seed (fruits) is abscised in a leafy sheath, the seed is shaken loose as wind blows the severed structure over grass and dune. Whole tumbleweed plants, such as *Sisymbrium atissimum* (tumbling mustard), mature, break at soil level and tumble in the wind across grass prairie and drop seed from siliques either intermittently as they tumble or when at a fence or other barrier.

Many conifers, elms, maples and many other plants have winged propagules, which, borne by wind, may be delivered several hundred metres from their parent plant. Wind may assist establishment of seed that falls into soil, cracks and crannies, because the wings or other appendages are hygroscopic and respond to changes in wind humidity and temperature to lengthen and contract thus driving the seed further into the subsoil. Watch the behaviour of the awns of *Stipa* spp. (needlegrass) in a light breeze. Wind can carry parachute "seeds" like those of *Tragopogon* spp. (yellow salsify) to elevations of several hundred metres and over low mountains. Balloon fruits such as those of *Physalis peruviana* (ground cherry), a common garden weed, may not travel so far in the wind but can effectively move from urban lot to urban lot. Dispersal is the subject of the comprehensive classic by Ridley (1930).

Wind: leaf surfaces and the boundary layer

The thin layer of air immediately adjacent to leaf surfaces does not behave in quite the same way as ambient air; it is usefully termed the "boundary layer". Boundary layer air is not quite motionless because it is held close to the leaf surface. It may be only a millimetre or two thick, a distance that varies from species to species and with the nature of the leaf surface. Leaf form (flat or needle-like), pubescence, venation, location next to upper or lower leaf surface, and the number and placement of stomata all affect the boundary layer. Gas exchange occurs at and through the semi-permeable protective cuticle and the boundary layer. This is also where leaf aroma and fragrance are generated, and where palatability and the flavour of foliage to all herbivores and omnivores are perceived. The wind distributes the greenhouse gases, carbon dioxide and methane, and water vapour, which contribute to the haze that develops over tropical rainforests and over some temperate latitude skies on hot summer days. The chemistry and physics of the boundary layer are difficult to study, but its gas composition is very complex and the number of chemicals in one fragrance may alone exceeded four hundred. Chemistry and physics aside, the astonishing diversity of leaf surfaces and variety of leaves is telling a story of immense importance to life on earth and also of a long evolutionary history of intimacy of plant and wind.

Wind and global warming

The temperature of land, sea and atmosphere is rising. Increasing atmospheric turbulence can be expressed as intensification of wind but unevenly; some feedback mechanisms may dampen the expression but in all likelihood winds overall will increase. To meet the challenge prudence is suggested. In a garden situation such as that on the UBC campus thinning and spiral pruning of woody vegetation or enhancing root systems may be useful; storm insurance with companies may be wise in many cities. The UK suffered devastating storms a few years ago and it is understood that Kew gardens and U K insurance companies are addressing the likelihood and impact of wind intensification.

Wind and plants make music

The article began with a reference to the poem, *The Wind Our Enemy*, and with a plea in numerous ways to also recognize it as a largely unappreciated friend to plants. Plants have evolved using the energetic wind–plants have been formed by it and damaged by it–truly both enemy and friend. Wind universal, is not simple in its relationships with plants: there is the wind we feel, the poetic or archaic wind, the wind understood best by poets, artists, photographers and naturalists.

If we sit beside a brook and listen to wind and plants make music near an aspen grove in the evening after a hot summer, we will hear the music of the Moldau; starting with wisps, gathering as a torrent when the cool winds slide down from mountain slope and then to join the stately Danube. If we stand in the boreal spruce forests in winter, we will hear Finlandia or we may linger in a field of grass and hear as Aldous Huxley did, "The Song of the Poplars". Pause and hearken to the music in the leafage.

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